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Phylogenetic origins and family classification of typhuloid fungi, with emphasis on *Ceratellopsis*, *Macrotyphula* and *Typhula* (Basidiomycota)

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Abstract: Typhuloid fungi are a very poorly known group of tiny clavarioid homobasidiomycetes. The phylogenetic position and family classification of the genera targeted here, *Ceratellopsis*, *Macrotyphula*, *Pterula sensu lato* and *Typhula*, are controversial and based on unresolved phylogenies. Our six-gene phylogeny with an expanded taxon sampling shows that typhuloid fungi evolved at least twice in the Agaricales (*Pleurotineae*, *Clavariineae*) and once in the *Hymenochaetales*. *Macrotyphula*, *Pterulicium* and *Typhula* are nested within the *Pleurotineae*. The type of *Typhula* (1818) and *Sclerotium* (1790), *T. phacorrhiza* and *S. complanatum* (synonym *T. phacorrhiza*), are encompassed in the *Macrotyphula* clade that is distantly related to a monophyletic group formed by species usually assigned to *Typhula*. Thus, the correct name for *Macrotyphula* (1972) and *Typhula* is *Sclerotium* and all *Typhula* species but those in the *T. phacorrhiza* group need to be transferred to *Pistillaria* (1821). To avoid undesirable nomenclatural changes, we suggest to conserve *Typhula* with *T. incarnata* as type. *Clavariaceae* is supported as a separate, early diverging lineage within Agaricales, with *Hygrophoraceae* as a successive sister taxon to the rest of the Agaricales. *Ceratellopsis* s. auct. is polyphyletic because *C. acuminata* nests in *Clavariaceae* and *C. sagittiformis* in the *Hymenochaetales*. *Ceratellopsis* is found to be an earlier name for *Pterulicium*, because the type, *C. queletii*, represents *Pterulicium gracile* (synonym *Pterula gracilis*), deeply nested in the *Pterulicium* clade. To avoid re-combining a large number of names in *Ceratellopsis* we suggest to conserve it with *C. acuminata* as type. The new genus *Bryopistillaria* is created to include *C. sagittiformis*. The families *Sarcomyaceae* and *Phyllotopsidaceae*, and the suborder *Clavariineae*, are described as new. Six new combinations are proposed and 15 names typified.

Key words: Agaricomycetes, basidioma evolution, *Clavariaceae*, clavarioid fungi, *Pleurotineae*, *Sclerotium*, *Typhulaceae*.

Taxonomic novelties: New suborder: *Clavariineae* Olariaga, Huhtinen, Læssøe, J.H. Petersen & K. Hansen, New family: *Phyllotopsidaceae* Locquin ex Olariaga, Huhtinen, Læssøe, J.H. Petersen & K. Hansen, *Sarcomyaceae* Olariaga, Huhtinen, Læssøe, J.H. Petersen & K. Hansen, New genus: *Bryopistillaria* Olariaga, Huhtinen, Læssøe, J.H. Petersen & K. Hansen, *New combinations:* *Bryopistillaria sagittiformis* (Pat.) Olariaga, Huhtinen, Læssøe, J.H. Petersen & K. Hansen, *Macrotyphula megasperma* (Berthier) Olariaga, Huhtinen, Læssøe, J.H. Petersen & K. Hansen, *Macrotyphula phacorrhiza* (Reichard: Fr.) Olariaga, Huhtinen, Læssøe, J.H. Petersen & K. Hansen, *Typhula podocarpus* (Crous) Olariaga, Huhtinen, Læssøe, J.H. Petersen & K. Hansen, **Typification:** **Lectotypification:** *Ceratella ferryi* Quél. & Fautrey, *Clavaria aculina* Quél., *Clavaria microscopica* Malbr. & Sacc., *Pistillaria aciculata* Durieu & Lév. ex Sacc., *Pistillaria aculeata* Pat., *Pistillaria acuminata* Fuckel, *Pistillaria attenuata* Syd. & P. Syd., *Pistillaria carestiae* Ces. in Bres. & Sacc., *Pistillaria equiseticola* Boud., *Pistillaria helenae* Pat., *Pistillaria juncicola* Bourdot & Galzin, *Pistillaria queletii* Pat., *Pistillaria sagittiformis* Pat., *Sclerotium complanatum* Tode, *Typhula brunaudii* Quél., **Epitypification:** *Pistillaria acuminata* Fuckel, *Pistillaria queletii* Pat., *Pistillaria sagittiformis* Pat., *Sclerotium complanatum* Tode.

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INTRODUCTION

Clavarioid fungi have club- or coral-shaped basidiomata with the hymenium fully exposed and include at least 540 species (Corner 1950, Kirk *et al.* 2008). Phylogenetic studies have demonstrated that clavarioid basidiomata have arisen multiple times from ancestors with agaricoid or corticioid basidiomata in several lineages of Basidiomycota (Pine *et al.* 1999, Dentinger & McLaughlin 2006), but molecular phylogenies of clavarioid fungi and allied taxa are far from being complete. Clavarioid lineages are known to have evolved in the Agaricales, *Cantharellales*, *Gomphales*, *Hymenochaetales*, *Russulales*, *Thelephorales* and *Trechisporales* among the Agaricomycetes (Pine *et al.* 1999, Hibbett & Binder 2002, Hibbett 2004, Dentinger & McLaughlin 2006, Birkebak *et al.* 2013), but fully supported multigene phylogenies are lacking in most cases and details as to how transitions to a clavarioid basidioma type have occurred are vague. A

more comprehensive taxon sampling and addition of more molecular markers is still needed in many groups, including clavarioid fungi, to better understand the evolution of basidioma configuration.

In this study, we target a group of clavarioid fungi with tiny basidiomata (Fig. 1A–K), here referred to as “typhuloid” following e.g. Corner (1950), Petersen (1974), Petersen *et al.* (2014), and Olariaga *et al.* (2016). Corner (1950: 145) characterised typhuloid fungi by their: i) small basidiomata and limited growth, ii) distinct stipe and fertile head, iii) simple hymenium, iv) epiphytic habitat on wood, stems or leaves, rather than being terricolous, v) smooth, white ellipsoid spores, vi) monomitic, generally clamped hyphae, and vii) agglutination of the hyphae on the surface of the stem. Three genera were regarded as typhuloid, *Typhula*, *Pistillaria* and *Pistillina* (Corner 1950), and were separated from pteruloid fungi (*Deflexula*, *Pterula*) with a dimitic hyphal system and from *Ceratellopsis* with highly reduced



Fig. 1. Diversity of typhuloid and pleurotoid fungi suggested to be closely related to *Typhula*. **A.** *Macrotyphula fistulosa* s.l. (IO.14.214, ARAN-Fungi). **B.** *Macrotyphula juncea* (IO.16.53, S). **C.** *Typhula phacorrhiza*, current type of *Typhula* (ARAN-Fungi 7446), here combined in *Macrotyphula*. **D.** Compressed sclerotium of *T. phacorrhiza* (ARAN-Fungi 7446). **E.** *Typhula incarnata*, showing sclerotia at the base (IO.14.92, S), proposed conserved type of *Typhula*. **F.** *Typhula uncialis* (IO.14.94, S, UPS), type of *Gliocoryne*. **G.** *Typhula crassipes* (IO.14.83, S, UPS). **H.** *Typhula subhyalina* (IO.15.06, S), type of *Pistillina* and *Dacryopsella*. **I.** *Typhula erythropus* (IO.16.83, ARAN-Fungi). **J.** *Ceratellopsis* aff. *aculeata* (ARAN-Fungi 11746). **K.** *Pterulicium gracile* (IO.14.142, S, UPS). **L.** *Phyllotopsis nidulans* (ARAN-Fungi). **M.** *Pleurocybella porrigens* (BIO-Fungi 13431). **N.** *Sarcomyxa serotina* (IO.14.130, S, UPS). Photographs I. Olariaga, except L by J.I. Iturriz.

clavarioid basidiomata with generally sterile apices. Berthier (1976), in his monograph “*Typhula* and allied genera”, treated typhuloid fungi in a broader sense and considered *Ceratellopsis*, *Macrotyphula*, *Pterula* and *Typhula* to represent a natural group without proposing any family classification. *Hirticlavula elegans*, a member of *Clavariaceae* producing minute, hairy basidiomata, has also been considered somewhat typhuloid (Petersen et al. 2014), and limits between typhuloid fungi and other reduced clavarioid fungi are not always clear. Typhuloid fungi represent one of the most overlooked, poorly known and enigmatic groups of homobasidiomycetes. The family classification of these fungi is uncertain or based on weakly supported phylogenies with a

very limited taxon sampling. *Macrotyphula* and *Typhula* were previously placed in *Clavariadelphaceae* (Corner 1970, Hawksworth et al. 1995), but recent classifications place both genera in *Typhulaceae* together with *Sclerotium* (Kirk et al. 2008, Knudsen & Vesterholt 2012). The family classification of *Ceratellopsis* is even more controversial. Initially included by Corner (1970) in *Clavariadelphaceae*, Jülich (1982) accommodated it in *Typhulaceae*. Hawksworth et al. (1995) and Begerow et al. (2018), probably following Corner, included it in *Gomphaceae*, although *Ceratellopsis* lacks the synapomorphic characters of this family, such as pistillarin, ampullate septa and cyanophilous, ornamented spores (Hosaka et al. 2006). As no

molecular data of *Ceratellopsis* has been available, its phylogenetic relationships and classification have remained doubtful. Besides the above-mentioned genera treated by Berthier (1976), *Mucronella* and *Hirticlavula*, both producing tiny clavarioid basidiomata, have been assigned to the *Clavariaceae* based on molecular data (Birkebak *et al.* 2013, Petersen *et al.* 2014). Regardless of their phylogenetic origin, all typhuloid fungi share similar taxonomic problems. For many species of those genera only the type specimen or very few collections are known, species limits are unclear and distribution data are meagre. Molecular data of only a handful of species are available in public sequence repositories and the high morphological diversity of the group remains poorly sampled.

Typhula* and segregated genera, *Macrotyphula*, and phylogenetic position of *Typhulaceae

The phylogenetic position of *Typhulaceae* has been inferred from only two species, *Typhula phacorrhiza* and *Macrotyphula fistulosa*, type of *Typhula* and *Macrotyphula*, respectively. Through analyses of a 5-locus dataset, Matheny *et al.* (2006) recovered *Typhulaceae* in the hygrophoroid clade (*Agaricales*) with phylogenetic confidence, as sister to the *Hygrophoraceae* in a supported clade encompassing *Pterulaceae* and members of two pleurotoid agaric genera (*Sarcomyxa serotina* and *Phyllotopsis* spp.) (Fig. 1L–N). Binder *et al.* (2010), employing a broader taxon sampling of the *Agaricomycetes*, recovered also *Typhulaceae* as sister to *Hygrophoraceae* but without support, while *Pterulaceae* was supported as closely related to *Stephanosporaceae* instead (Binder *et al.* 2010). Other studies have not been able to confirm or reject the inclusion of *Typhulaceae* in the hygrophoroid clade, but recovered agaric or pleurotoid genera, such as *Phyllotopsis*, *Pleurocybella*, *Tricholomopsis*, as sister taxa of *Typhulaceae* with phylogenetic confidence (Dentinger & McLaughlin 2006, Lodge *et al.* 2014). Dentinger *et al.* (2016) resolved for the first time several deep nodes of the *Agaricales* through a 208-locus dataset containing 35 taxa of *Agaricales*, and found that the hygrophoroid clade, as defined by Matheny *et al.* (2006), was paraphyletic. Also, *Hygrocybe conica* (*Hygrophoraceae*) was recovered as sister to the *Clavariaceae*, while *Pterulaceae* (*Pterula multifida*; recovered in the hygrophoroid clade by Matheny *et al.* (2006)), appeared in a branch with *Pleurotus ostreatus*. Thus, the results by Dentinger *et al.* (2016) question the inclusion of the *Typhulaceae* in the hygrophoroid clade. In addition to its uncertain phylogenetic position, the monophyly of *Typhulaceae* has not been tested appropriately.

Two genera, *Typhula* and *Macrotyphula*, are currently accepted in *Typhulaceae* (e.g. Berthier 1976, Knudsen & Vesterholt 2012). *Macrotyphula* differs from *Typhula* in having large, yellow-brown basidiomata (30–300 mm) that never arise from sclerotia and non-amyloid spores (Berthier 1976). In contrast, *Typhula* includes species with smaller basidiomata (generally under 10 mm long) that often arise from sclerotia and usually have amyloid spores. Some *Typhula* species are important plant pathogens that cause economic loss in cereal crops (e.g. Ekstrand 1955). These are popularly known as “snow moulds”, producing symptoms known as “Typhula blight” (Matsumoto *et al.* 2001, Hoshino *et al.* 2008). Several economically important species like *T. incarnata* and *T. ishikariensis* have been subjected to extensive research on

their ecology, physiology and genetics (e.g. Matsumoto 1992, Vergara *et al.* 2004, Blunt *et al.* 2015, Chang 2015, Koch 2016). Generic limits of *Typhula* are not fully delineated and lack a complete consensus. Probably due to the fact that its species show diverse basidioma morphologies, sclerotial anatomy and asexual morph states (Berthier 1976), a number of genera have been segregated from *Typhula*, such as *Cnazonaria*, *Dacryopsella*, *Gliocoryne*, *Phacorrhiza*, *Pistillaria*, *Pistillina*, *Scleromitra* and *Sphaerula*. These genera have been used to a certain extent. Of these, Corner (1950) recognised *Pistillaria* (with *Cnazonaria*, *Gliocoryne*, *Scleromitra* and *Sphaerula* in synonymy), *Pistillina* and *Typhula* (with *Phacorrhiza* in synonymy). Donk (1954) adopted also *Pistillaria*, *Typhula* and *Pistillina*, and further synonymised *Dacryopsella* under *Pistillina*. *Pistillaria* has been recognised generally based on a ceraceous consistency of the fresh fruitbodies, horny when dried, and the absence of sclerotia (Corner 1950, 1970, Pilát 1958), but generic limits between *Pistillaria* and *Typhula* have been long debated (Corner 1950, Bourdot & Galzin 1928, Donk 1954, Berthier 1976). *Pistillina* has been distinguished by basidiomata with a globose fertile part (Corner 1950). Berthier (1976), after examining extensive material and type specimens available, merged all these genera under *Typhula* (*Sphaerula*, *Scleromitra* and *Dacryopsella* were not treated in the monograph), but recognised *Cnazonaria*, *Gliocoryne*, *Pistillaria* and *Pistillina* as subgenera. After the publication of Berthier's monograph, a few authors have continued to use *Pistillaria* and *Pistillina* at the generic level (Shiryaev & Kotiranta 2007, Kaygusuz & Çolak 2017, Begerow *et al.* 2018, Petersen & Læssøe 2019). Recently, the new monotypic genus *Tygervalleomyces* was described in *Typhulaceae* based on analyses of the 28S region (Crous *et al.* 2017). The asexual morph of *Tygervalleomyces podocarpi*, the only known morph, is similar to the asexual morph of *Typhula crassipes* (Berthier 1976, as *Typhula corallina*) in the cylindrical conidia with a truncate base, and in fact these two species have highly similar 28S sequences (98 %) and nested within a larger highly supported clade containing other *Typhula* species (Crous *et al.* 2017). In view of this, the status of *Tygervalleomyces* needs to be re-evaluated in the light of a phylogeny with a broader sampling of *Typhula* species. Olariaga & Salcedo (2013) synonymised *Typhula* and *Macrotyphula* due to the fact that *T. phacorrhiza* formed a monophyletic group with *Macrotyphula* in previous analyses (Pine *et al.* 1999, Hibbett 2007), as well as morphological similarities. The designation of *T. phacorrhiza* as lectotype of *Typhula* by Donk (1933) has been considered unfortunate (Berthier 1976, Olariaga 2009, Olariaga & Salcedo 2013), because *T. phacorrhiza*, with long filiform basidiomata and unique compressed sclerotia, is an atypical species in *Typhula* (Remsberg 1940, Corner 1950, Berthier 1976). In fact, *T. phacorrhiza* shares many features with *M. fistulosa*, i.e. the pale brown, large basidiomata, the stipe surface with thin hyphae and caulotrichomes, the basal tomentum formed by thick-walled, scarcely septate hyphae and the presence of a hyaline, striped encrustation on the medulla hyphae (Olariaga & Salcedo 2013). Molecular phylogenetic analyses show that these species are closely related and nested in the *Agaricales* (Binder *et al.* 2010). Nevertheless, taxon sampling in phylogenetic studies of *Typhulaceae* is extremely poor and the synonymy of *Typhula* and *Macrotyphula* needs to be further explored.

The type of *Sclerotium* is conspecific with the type of *Typhula*

The genus *Sclerotium*, also included in *Typhulaceae* (Kirk *et al.* 2008), is currently treated as an artificial genus that accommodates fungi producing sclerotia but not, or rarely, a sexual morph (Xu *et al.* 2010). Tode (1790) included originally eight species in *Sclerotium*, of which Fries (1821) treated *S. complanatum* in the first place and Clements & Shear (1931: 411) thus selected this species as the type of *Sclerotium*. A number of authors, especially during the XIXth century, described numerous species in *Sclerotium*, including ascomycetous and basidiomycetous fungi (e.g. Fries 1822, Léveillé 1843, Duby 1830, Desmazières 1848, Rostrup 1866), and numerous plant pathogens (Xu *et al.* 2010). Until now, 464 names have been described or combined in *Sclerotium* (Index Fungorum, viewed on 11 June 2019) and it is evident that species assigned to *Sclerotium* have multiple evolutionary origins, but very few attempts to disassemble it have been made (Xu *et al.* 2010). With the end of the asexual-sexual morph dual nomenclature, many names in *Sclerotium* may turn out to have priority over species names in use. Several early authors observed that some *Sclerotium* species appeared in connection or directly attached to basidiomata of *Typhula* species (e.g. Berkeley 1837, Léveillé 1843 (as *Clavaria*), Rostrup 1866). *Sclerotium complanatum*, type of *Sclerotium*, is characterised by producing compressed sclerotia attached to the substrate by a small stalk (Tode 1790) which conform to those produced by *T. phacorrhiza* (Berkeley 1837, Rostrup 1866, Schröter 1889). Thus, it is generally accepted that *S. complanatum* is a synonym of *T. phacorrhiza* (Xu *et al.* 2010, Kaygusuz & Çolak 2017), although only Remsberg (1940) has proposed this synonymy according to our search. Other authors attributed *S. complanatum* to the sclerotial morph of *T. gyrans* (Fries 1874, Corner 1950, Donk 1962), but this view appears to have been abandoned. In the meantime, the taxonomic identity of *S. complanatum* has not been reassessed and the name remains untypified. As currently asexual names compete with sexual names for priority, the possible synonymy of *S. complanatum* and *T. phacorrhiza* would make *Sclerotium* and *Typhula* taxonomic synonyms, and all *Typhula* names in use, including those being applied to economically important plant pathogens, would have to be transferred to the older and equally sanctioned genus *Sclerotium*. Examining in depth the taxonomic concept of *S. complanatum* and proposing a typification is thus of paramount importance to deal with a possible scenario of undesirable nomenclatural changes.

The poorly known genus *Ceratellopsis*, a possible earlier synonym of *Pterulicium*

Ceratellopsis differs from *Typhula* in having minute filiform basidiomata with a sterile apex and a non-corticate stipe (Corner 1950, Berthier 1976). Short basidia up to 20 µm have also been suggested to be a diagnostic character (Jülich 1982). *Pterulicium gracile*, called *Pterula gracilis* until very recently (Leal-Dutra *et al.* 2020), strongly resembles species of *Ceratellopsis* because of its minute white basidiomata with a sterile apex, at least at early stages of development (Corner 1950, Berthier 1976), but it differs microscopically in having skeletal hyphae, typical for

Pterulaceae, 2-spored basidia and no stipe (Corner 1950, Olariaga 2009). Furthermore, we have made collections with very minute basidiomata with a clearly delimited stipe suggesting *Ceratellopsis*, but having skeletal hyphae as typical in *Pterulaceae*. Limits between *Ceratellopsis* and *Pterulaceae*, thus, are not always clear-cut.

As pointed out by Donk (1954), Konrad & Maublanc (1937) introduced *Ceratellopsis* based on the validly published but illegitimate *Ceratella* Pat. (Patouillard 1887; later homonym of *Ceratella* Hook. f. 1844) and explicitly indicated *Ceratellopsis queletii* as the type of *Ceratellopsis*. While Donk (1954) followed this typification, Corner (1950), noted that *C. queletii* might represent a rudimentary *Pterula*, and he selected instead *Ceratellopsis aculeata* as type so that *Ceratellopsis* could be used with certainty and not reduced to a synonym of *Pterula*. This choice, nevertheless, is not permissible (Turland *et al.* 2018; Art. 7.8) since the original type indication of *Ceratellopsis* by Konrad & Maublanc (1937) is unequivocal and irrevocable. Also, Olariaga (2009) proposed tentatively that *C. queletii* might be a synonym of *Pterulicium gracile*, but up to present, no consistent and stable interpretation of *C. queletii* has been provided and the taxonomic status of *Ceratellopsis* remains unresolved. Twenty-four names have been described or combined in *Ceratellopsis*, but several of them represent *P. gracile* (Berthier 1976) or *Typhula* species.

The confirmation that *C. queletii*, type of *Ceratellopsis*, is a synonym of *P. gracile* would have important consequences in the classification of *Pterulaceae*. The family, centered on the genus *Pterula*, has included several clavarioid genera with a dimitic hyphal system (Corner 1970). Based on molecular studies, four resupinate genera (*Aphanobasidium*, *Coronicium*, *Merulicium*, *Radulomyces*; Larsson 2007, Larsson *et al.* 2004) and the polyporoid *Radulotubus* (Zhao *et al.* 2016) were later transferred to *Pterulaceae*. In the light of analyses of the ITS, 28S and RPB2 regions, employing a rich taxon sampling of the *Pterulaceae*, Leal-Dutra *et al.* (2020) elucidated generic limits in the family. This study discovered *Pterula* to be polyphyletic and splits its species into the new genus *Myrmepterula*, *Phaeopterula* and *Pterulicium*, leaving in *Pterula sensu stricto* a handful of species around *Pterula plumosa*. *Deflexula* was shown to be paraphyletic because some species nest in the *Pterula* clade, while the type *D. fascicularis* is in the *Pterulicium* clade. In total, 46 names earlier treated in *Pterula* and *Deflexula* were combined in *Pterulicium*, a genus up to then monospecific. *Pterula gracilis* was found to belong to the *Pterulicium* clade and accordingly combined as *Pterulicium gracile*. In this framework, would the synonymy between *C. queletii* and *P. gracile* be confirmed, the name *Ceratellopsis* (1937) would have priority over *Pterulicium* (1950). Thus, the identity of *C. queletii* needs urgent clarification.

In the present study, we expand the taxon sampling of typhuloid fungi based on the multigene datasets used by Matheny *et al.* (2006) and Binder *et al.* (2010). With these data, our main goals were to: 1) provide a robust phylogenetic hypothesis for typhuloid fungi, especially for *T. phacorrhiza* (type of *Typhula*), types of genera segregated from *Typhula*, *Sclerotium complanatum* (type of *Sclerotium*) and *Ceratellopsis* species; 2) test the monophyly of *Typhula*; 3) assign typhuloid fungi to appropriate families; and 4) propose an updated nomenclature in the light of a robust multigene phylogeny.

MATERIAL AND METHODS

Molecular techniques

DNA was extracted from fresh (stored in 1 % SDS extraction buffer) basidiomata, using a DNeasy Plant Mini Kit (Qiagen) according to the manufacturer's instructions. The following six gene regions were amplified: 1) nu5.8S rDNA, the 5' end of the nuclear 28S rDNA (spanning domains D1–D2), part of the nuSSU rDNA (ca. 1 600 bp), *RPB1* (900 bp; A–C), *RPB2* (5–7 region, ca. 1 100 bp) and *EF-1α* (1 100 bp). The ITS (ITS1–5.8S–ITS2) and 28S regions were amplified in one piece using the primers ITS5-LR7, or otherwise as separate pieces: ITS using ITS5-ITS4, (White *et al.* 1990); and 28S using LR0R-LR5 (or LR3) and LR3R-LR7 (Vilgalys & Hester 1990). The same primers were used for sequencing. The ITS was sequenced using the primers ITS1-ITS4 and/or in a few instances ITS5, 5.8S and ITS3. The SSU region was amplified in one piece employing primers NS1-NS8 or in two pieces using NS1-NS4 and NS3-NS8 (White *et al.* 1990). PCR products of the *RPB1* region were obtained using gRPB1-A (Stiller & Hall 1997) and fRPB1-C rev primers (Matheny *et al.* 2002). The sequence spanning *RPB2* regions 5–7 was amplified in one piece, using fRPB2-5F and bRPB2-7R, or if required, in two pieces with primers fRPB2-5F-gRPB2-6R and bRPB2-6F-bRPB2-7R (Liu *et al.* 1999, Matheny 2005). For samples that did not successfully amplify or for sequencing, *Typhula*-specific primers were designed for the *RPB2* region and used in different combinations (Table 1). The *EF-1α* region was PCR amplified and sequenced employing 983F and 2218R primers (Rehner & Buckley 2005). *Typhula*-specific primers of the *EF-1α* region were designed and used for PCR amplification and sequencing of problematic samples (Table 1). PCR amplifications were performed using Illustra™ Hot Start Mix RTG PCR beads (GE Healthcare, UK) in a 25 µL volume, containing 3 µL of genomic DNA, 10 µM of each primer and distilled water. PCRs were conducted in Applied Biosystems GeneAmp® PCR System 9700 and 2720 Thermal Cyclers. Amplifications were performed using the following program: initial denaturation at 95 °C for 5 min, followed by 35–40 cycles of 95 °C for 45–60 s, 52–58 °C for 50 s, 72 °C for 1 min, followed by a final extension at 72 °C for 10 min. PCR amplifications of protein-coding genes follow O'Donnell *et al.* (2011, *RPB1*) and Hansen *et al.* (2013, *RPB2*, *EF-1α*). PCR products were purified using the enzymatic method Exo-sap-IT (USB Corporation, Santa Clara, California, USA). When multiple bands were amplified in the *RPB1* and *RPB2* regions, PCR products were

size-fractionated in a 1 % agarose gel, stained with GelRed™ (Biotium Inc.), visualised over a UV trans-illuminator, excised and purified using QIAquick spin columns (Qiagen). Purified PCR products were sequenced at Macrogen Europe service (www.macrogen.com).

Type specimens, taxon and molecular sampling

Type specimens of small typhuloid fungi available at E, FH, M, PC, S and UPS herbaria were examined: *Ceratella ferryi*, *Ceratellopsis carestiae*, *C. rickii*, *C. acuminata*, *C. equiseticola*, *Clavaria aculina*, *C. microscopica*, *Pistillaria attenuata*, *P. juncicola*, *Pterulicium gracile*, *Typhula brunaudii*, *T. crassipes*, *T. sclerotoides*, *T. sphaeroidea*, *T. subhyalina* and *T. uncialis*. Material deposited in G (customs blocked the loan), PAD (not available on loan) and SAPA (several contact attempts unsuccessful) could not be examined. The notation “!” indicates that type or other original material was examined by us. Cultures of the taxa collected and described in this study were deposited in the CBS-KNAW culture collection at the Westerdijk Fungal Biodiversity Institute.

For molecular analyses, types and other species of genera considered to be typhuloid or assigned to *Typhulaceae* were sampled, namely *Ceratellopsis*, *Macrotyphula*, *Pterulicium gracile*, *Typhula* s.l. and *Sclerotium*. A collection identified as *C. acuminata*, with skeletal hyphae, was included to test the limits between *Ceratellopsis* and *Pterula*. Nucleotide sequences were aligned in the six-gene dataset (nu5.8S rDNA, nu28S rDNA, nu18S rDNA, *RPB1*, *RPB2* and *EF-1α*) assembled by Binder *et al.* (2010; TreeBASE no. S10185), in order to preliminarily explore their phylogenetic affinities. Nucleotide sequences were aligned in Ali-view (Larsson 2014). This alignment was subjected to a maximum likelihood (ML) analysis using the “RAxML HPC2 on XSEDE” tool (Stamatakis 2014) in the CIPRES Science Gateway (Miller *et al.* 2010), starting from a random tree. A GTR-GAMMA model with four rate categories was selected for tree inference. For branch confidence, 1 000 ML bootstrap replicates were conducted with a GTRCAT model (ML-BP). Targeted typhuloid taxa nested in *Agaricales* (ML-BP 92 %), except for *Ceratellopsis sagittiformis* that was placed in *Hymenochaetales*. Based on this analysis, a first 6-locus (5.8S, 28S, 18S, *RPB1*, *RPB2*, *EF-1α*) dataset (the *Agaricales* matrix) was prepared to phylogenetically place typhuloid fungi among the *Agaricales*. Three taxa, *Amylocorticium cebennense*, *Plicaturopsis crispa* and *Serpulomyces borealis*, were included as outgroup for rooting purposes based on previous studies (Binder *et al.* 2010). A second dataset with the same molecular markers (the *Pleurotineae* matrix) included *Typhulaceae*

Table 1. Newly designed *Typhula*-specific primers for the *RPB2* and *EF-1α* (5'–3') regions.

Locus	Primer	Sequence	PCR	Sequencing
<i>EF-1α</i>	1007F-Typh	SCGAGGAYCGTTTCAACGAG		X
<i>EF-1α</i>	1447F-Typh	GCATGCCHTGGTWCAGG	X	X
<i>EF-1α</i>	1825F-Typh	GAACGTVTCCTGTYAAGGAYA		X
<i>EF-1α</i>	2100R-Typh	ATKGGCTTGGARGGRACRA		X
<i>RPB2</i>	RPB2-5Fint-Typh	AARAARCGDYTNNGAYYTS GC		X
<i>RPB2</i>	RPB2-6F-Typh	TGGGGAYTGGAGTCGTTGGA	X	X
<i>RPB2</i>	RPB2-6R-Typh	TCCAACGACTCCARTCCCCA	X	X
<i>RPB2</i>	RPB2-7Rint-Typh	TASGTGTTACGAGGRGACT		X

Table 2. Sequenced specimens used in this study, with GenBank accession numbers for 5.8S, 28S, 18S, *RPB1*, *RPB2* and *EF-1α* regions. Numbers in parentheses following the species names indicate multiple collections of a species. The GenBank accessions of sequences generated in this study are in **bold**. Asterisks indicate sequences obtained from genome data through the JGI portal (<https://jgi.doe.gov/>). Abbreviations of datasets are: ag = *Agaricales*, cl = *Clavariineae*; hy = *Hymenochaetales*, pl = *Pleurotineae*.

Original name	Updated name	Voucher specimen	Dataset	GenBank accession numbers					
				5.8S	28S	18S	<i>RPB1</i>	<i>RPB2</i>	<i>EF-1α</i>
<i>Agaricus bisporus</i> *	—	H97	ag	Genome	Genome	Genome	genome	Genome	genome
<i>Alloclavaria purpurea</i>	—	PBM 2731 (CUW)	hy	DQ486690	DQ457657	DQ437679	—	—	—
<i>Anomoporia bombycina</i>	—	CFMR:L-6240	cl	—	GU187564	—	—	—	—
<i>A. kamtschatica</i>	—	GB/M Edman K426	cl	—	DQ144615	—	—	—	—
<i>Anthracoophyllum archeri</i>	—	PBM 2201 (WTU)	ag	DQ444308	AY745709	DQ092915	DQ435799	DQ385877	DQ028586
<i>Amanita brunnescens</i>	—	PBM 2429 (CUW)	ag	AY789079	AY631902	AY707096	AY788847	AY780936	AY881021
<i>Aphanobasidium pseudotsugae</i>	—	HHB-822 (CFMR)	ag, pl	GU187509	GU187567	GU187620	GU187695	GU187781	GU187695
<i>Armillaria mellea</i>	—	PBM 2470 (CUW)	ag	AY789081	AY700194	AY787217	AY788849	AY780938	AY881023
<i>Baeospora myosura</i>	—	PBM 2748 (CUW)	ag	DQ484063	DQ457648	DQ435796	DQ435801	DQ470827	GU187762
<i>Basidioradulum radula</i>	—	GEL 2493 (KASSEL)	hy	DQ234537	AY700184	AY771611	—	—	—
<i>Blasiphalia pseudogrisella</i>	—	P. Hoijer 4393 (H7031951)/ IO.14.231 (S)	hy	MF319048	MF318899	MF318990	—	MT24239	—
<i>Bolbitius vitellinus</i>	—	MTS 5020 (WTU)	ag	DQ200920	AY691807	AY705955	DQ435802	DQ385878	DQ408148
<i>Camarophylloopsis schulzeri</i>	—	S. Jacobsson 3453 (H)	cl	—	AM946415	—	—	—	—
<i>Cantharelloopsis prescotii</i>	—	I. Kytovuori 08-0808/ H6059300	hy	MF319050	MF318901	MF318992	—	MF288855	—
<i>Cantharocybe gruberi</i>	—	PBM 510 (WTU)	ag, pl	DQ200927	DQ234540	DQ234546	DQ435808	DQ385879	DQ059045
<i>Ceratellopsis acuminata</i>	—	CBS 146691	ag, cl	MT232347	MT232298	MT232493	MT24236	MT24230	MT242352
<i>C. aculeatea</i>	—	ARAN-Fungi 13729	cl	—	MT232300	—	—	—	—
<i>C. aff. acuminata</i>	—	ARAN-Fungi 11746	cl	MT232348	MT232299	—	—	—	—
<i>C. sagittiformis</i> (1)	<i>Bryopistillaria sagittiformis</i>	IO.15.41 (S)	hy	—	MT232301	—	—	MT24231	—
<i>C. sagittiformis</i> (2)	<i>B. sagittiformis</i>	IO.15.85 (S)	hy	—	MT232302	—	—	MT24232	—
<i>C. sagittiformis</i> (3)	<i>B. sagittiformis</i>	IO.14.164 (S)	hy	MT232349	MT232303	—	—	MT24233	—
<i>Cheimonophyllum candidissimum</i>	—	PBM 2411 (WTU)	ag	DQ486687	DQ457654	DQ435812	DQ447888	DQ470831	GU187760
<i>Calocera comea</i>	—	GEL 5359 (KASSEL)	hy	AY789083	AY701526	AY771610	—	AY536286	—
<i>Clavaria acuta</i> (1)	—	RHP55840 (TENN043602)	cl	—	HQ877681	—	—	—	—
<i>C. acuta</i> (2)	—	MTS4577 (WTU)	cl	—	HQ877679	—	—	—	—
<i>C. acuta</i> (3)	—	JFA10440 (WTU)	cl	—	HQ877680	—	—	—	—
<i>C. alboglobospora</i>	—	TENN042295	cl	—	HQ877682	—	—	—	—
<i>C. argillacea</i>	—	TFB10720 (TENN058804)	cl	—	HQ877683	—	—	—	—
<i>C. australiana</i>	—	ADM1311 (TENN051311)	cl	—	HQ877685	—	—	—	—

Table 2. (Continued).

Original name	Updated name	Voucher specimen	Dataset	GenBank accession numbers					
				5.8S	28S	18S	RPB1	RPB2	EF-1 α
<i>C. aff. fragilis</i>	—	SAT98-349-01 (WTU)	cl	—	HQ877688	—	—	—	—
<i>C. fumosa</i>	—	GG_151003	cl	—	EF535268	—	—	—	—
<i>C. fuscata</i>	—	RHP55840 (TENN043602)	cl	—	HQ877681	—	—	—	—
<i>C. inaequalis</i>	—	MB 04-016 (WTU)	cl	—	AY745693	—	—	—	—
<i>C. pullei</i>	—	KGN98	cl	—	AY586646	—	—	—	—
<i>C. cf. rubicundula</i>	—	TENN043695	cl	—	HQ877697	—	—	—	—
<i>Clavaria</i> sp.(1)	—	TFB11835 (TENN060720)	cl	—	HQ877692	—	—	—	—
<i>Clavaria</i> sp.(2)	—	JMB10061001 (TENN065665)	cl	—	HQ877684	—	—	—	—
<i>C. stegasauroides</i>	—	PBM3373	cl	—	HQ877698	—	—	—	—
<i>C. zollingeri</i>	—	JMB08040912 (TENN064095)	cl	—	HQ877700	—	—	—	—
<i>Clavicornia taxophila</i>	—	9186	cl	—	AF115333	—	—	—	—
<i>Clavulinopsis amoena</i>	—	PBM3381	cl	—	HQ877702	—	—	—	—
<i>C. corallinosacea</i>	—	PBM3380	cl	—	HQ877707	—	—	—	—
<i>C. fusiformis</i>	—	MGW672 (TENN064110)	cl	—	HQ877717	—	—	—	—
<i>C. sulcata</i>	—	PBM3379	cl	—	HQ877709	—	—	—	—
<i>Clitocella mundula</i>	—	TJB 7599 (CORT)	ag	DQ494694	AY700182	DQ089017	DQ447937	DQ474128	—
<i>C. candicans</i>	—	WTU	ag	DQ202268	AY645055	AY771609	DQ447891	DQ385881	DQ408149
<i>C. subditopoda</i>	—	WTU	ag	DQ202269	AY691889	AY771608	DQ447892	AY780942	DQ408150
<i>Coltricia perennis</i>	—	P. Salo 11024 (H)	hy	MF319056	MF318907	MF318996	—	MF288856	—
<i>Collybia tuberosa</i>	—	TENN 53540	ag	AY854072	AY639884	AY771606	AY857982	AY787219	AY881025
<i>Conocybe lactea</i>	—	PBM 2411 (WTU)	ag	DQ486693	DQ457660	DQ437683	DQ447893	DQ470834	—
<i>Coprinus comatus</i>	—	ECV 3198 (UC)	ag	AY854066	AY635772	AY665772	AY857983	AY780934	AY881026
<i>Coprinopsis cinerea</i> *	—	AmutBmut #326	ag	genome	Genome	genome	genome	genome	genome
<i>Coronicium alboglaucum</i>	—	NH4208	pl	AY463400	AY586650	—	—	—	—
<i>Cortinarius iodes</i>	—	WTU	ag	AF389133	AY702013	AY771605	AY857984	AY536285	AY881027
<i>Cotylidia</i> sp.	—	WTU	hy	AY854079	AY629317	AY705958	—	AY883422	—
<i>C. undulatea</i>	—	IO.15.126 (S)	hy	MT232350	MT232304	—	—	MT24234	—
<i>Crepidotus cf. applanatus</i>	—	PBM 717 (WTU)	ag	DQ202273	AY380406	AY705951	AY333303	AY333311	DQ028581
<i>Cristinia</i> sp.	—	FP-100305 (CFMR)	pl	GU187526	GU187585	GU187637	GU187470	GU187793	GU187718
<i>Entoloma prunuloides</i>	—	TJB 4765 (CORT)	ag	DQ206983	AY700180	AY665784	DQ447898	DQ385883	DQ457633

(continued on next page)

Table 2. (Continued).

Original name	Updated name	Voucher specimen	Dataset	GenBank accession numbers					
				5.8S	28S	18S	RPB1	RPB2	EF-1 α
<i>Globulicium hiemale</i>	—	Hjm 19007 (GB)	hy	DQ873595	DQ873595	DQ873594	—	—	—
<i>Gymnopus contrarius</i>	—	PBM 2711 (WTU)	ag	DQ486708	DQ457670	DQ440643	DQ447902	DQ472716	GU187700
<i>Gyrophlexus brevibasidiata</i>	—	IO.14.230 (S)	hy	MT232351	MT232305	—	—	MT24235	—
<i>Fibricium rude</i>	—	GEL 2121 (KASSEL)	hy	—	AY700202	AY654888	—	—	—
<i>Fistulina Antarctica</i>	—	— (AFTOL-ID 1335)	ag	DQ486702	AY293181	AY293131	DQ447899	DQ472713	GU187698
<i>Flammulina velutipes</i>	—	TENN 52002	ag	AY854073	AY639883	AY665781	AY858966	AY786055	AY883423
<i>Hemimycena gracilis</i>	—	PBM 2715 (WTU)	ag	DQ490623	DQ457671	DQ440644	DQ447905	DQ472719	GU187709
<i>Hirticlavula elegans</i>	—	JHP-13.364 (O)	cl	—	KJ939349	—	—	—	—
<i>Hodophilus aff. foetens</i>	—	ECV4175 (TENN065670)	cl	—	HQ877678	—	—	—	—
<i>Hodophilus hymenoccephalus</i> (1)	—	WTU	cl	—	DQ457679	—	—	—	—
<i>H. hymenoccephalus</i> (2)	—	DJL98_081505	cl	—	EF561628	—	—	—	—
<i>Hohenbuehelia tremula</i>	—	PBM 2301 (WTU)/ DAOM 180808	pl	DQ182504	KU355405	DQ440645	—	KU355434	KU355465
<i>Hydropus cf. scabripes</i>	—	WTU	ag	DQ404389	DQ411536	DQ444855	DQ447908	DQ457634	—
<i>Hygrocybe coccinea</i>	—	PBM 915 (WTU)	ag, cl	DQ490629	DQ457676	DQ444858	DQ447910	DQ472723	GU187705
<i>H. aff. conica</i>	—	CBS 300.56	cl	—	DQ534589	—	—	—	—
<i>Hygrophorus pudorinus</i>	—	PBM 2721 (WTU)	ag	DQ490631	DQ457678	DQ444861	DQ447912	DQ472725	GU187710
<i>Hyphodontia alutaria</i>	—	KHL 11889 (GB)	hy	DQ873603	DQ873603	DQ873602	—	—	—
<i>Hyphodontiella multiseptata</i>	—	Ryberg 021022 (GB)	cl	—	EU118634	—	—	—	—
<i>Inocybe myriadophylla</i>	—	JV 19652F (WTU)	ag	DQ221106	AY700196	AY657016	DQ447916	AY803751	DQ435791
<i>Inotus griseus</i>	—	Dai 13436	hy	KX674583	KX364823	—	—	KX364919	—
<i>Infundibulicybe gibba</i>	—	JCS 0704B (WTU)	ag	DQ490635	DQ457682	DQ115780	DQ447913	DQ472727	GU187759
<i>Kneiffiella subalutacea</i>	—	KHL 11888 (GB)	hy	DQ873630	DQ873631	DQ873629	—	—	—
<i>Kuehneromyces rostratus</i>	—	PBM 2703 (WTU)	ag	DQ490638	DQ457684	DQ457624	DQ447918	DQ472730	GU187712
<i>Laccaria bicolor</i> *	—	S238N	ag	genome	genome	genome	genome	genome	genome
<i>Lachnella villosa</i>	—	CBS 609.87	ag	DQ097362	DQ097347	AY705959	—	DQ472732	GU187721
<i>Leifia flabelliradiata</i>	—	KG Nilsson 36270 (GB)	hy	DQ873635	DQ873635	—	—	—	—
<i>Lepista irina</i>	—	PBM 2291 (WTU)	ag	DQ221109	DQ234538	AY705948	DQ447919	DQ385885	DQ028591
<i>Lycoperdon pyriforme</i>	—	DSH 96-054 (WTU)	ag	AY854075	AF287873	AF026619	AY860523	AY218495	AY883426
<i>Macrolepiota dolichaula</i>	—	HKAS	ag	DQ221111	DQ411537	AY771602	DQ447920	DQ385886	DQ435785
<i>Macrotyphula fistulosa</i> (1)	—	IO.14.219 (S)/ IO.15.123 (ARAN-Fungi, S)/ TUB 011469	ag	—	DQ071735	MT232494	DQ068002	MT24236	MT242353

Table 2. (Continued).

Original name	Updated name	Voucher specimen	Dataset	GenBank accession numbers					
				5.8S	28S	18S	RPB1	RPB2	EF-1 α
<i>M. fistulosa</i> (2)	—	IO.14.214 (ARAN-Fungi, S)	ag	MT232352	KY224088	MT232495	MT24237	—	MT242354
<i>M. juncea</i> s.l.	—	IO.14.177 (S)	ag	MT232353	MT232306	MT241267	—	MT24237	MT242355
<i>Megacollybia platyphylla</i>	—	TENN 59432	ag	DQ249275	AY702016	AY786053	DQ447923	DQ385887	DQ435786
<i>Mucronella calva</i> (1)	—	JS16142	cl	—	AY586689	—	—	—	—
<i>M. calva</i> (2)	—	GEL4458	cl	—	AJ406588	—	—	—	—
<i>M. aff. calva</i>	—	KHL10317	cl	—	AY586690	—	—	—	—
<i>M. flava</i>	—	IO.16.84 (S)	ag, cl	MT232354	MT232307	MT232496	MT24238	—	MT242356
<i>M. fusiformis</i>	—	DJM 1309	ag, cl	—	DQ284905	—	—	—	—
<i>M. pendula</i>	—	PBM 3437	ag, cl	—	HQ829921	—	—	—	—
<i>Muscinipta laevis</i>	—	V. Haikonen 19745 (H6059292)	hy	MF319066	MF318921	MF319004	—	MF288861	—
<i>Mycetinis alliaceus</i>	—	TENN 55620	ag	AY854076	AY635776	AY787214	AY860526	AY786060	AY883431
<i>Odonticum romellii</i>	—	KHL s. n. (GB)	hy	DQ873639	DQ873639	DQ873638	—	—	—
<i>Onnia scaura</i> *	—	P53A	hy	genome	Genome	genome	—	genome	—
<i>Oxyporus populinus</i>	—	Dai 12793/ DSH 93-188	hy	KF111019	KF111021	AF026616	—	KT210380	—
<i>Peniophorella praetermissa</i>	—	GEL 2182 (KASSEL)	hy	AY854081	AY700185	AY707094	—	AY787221	—
<i>P. pubera</i>	—	KHL 13154 (GB)	hy	DQ873599	DQ873599	DQ873598	—	—	—
<i>Pluteus romellii</i>	—	ECV 3201 (UC)	ag	AY854065	AY634279	AY657014	AY862187	AY786063	AY883433
<i>Phaeomarasmius proximans</i>	—	PBM 1951 (WTU)	ag	DQ404381	AY752970	AY752970	—	AY333314	DQ028592
<i>Phellinidium ferrugineofusum</i> *	—	SpK3Phefer14	genome	genome	genome	genome	—	genome	—
<i>Phellinus tremulae</i>	—	KCTC 6659/ NJB2011-PT2-F	hy	AY189703	KU139202	AY178026	KU139277	—	—
<i>Phyllotopsis nidulans</i>	—	IO.14.196 (S)	ag, pl	—	MT232308	MT232497	MT24239	MT24238	MT242357
<i>Phyllotopsis</i> sp.	—	MB 35 (WTU)	ag, pl	DQ404382	AY684161	AY707090	DQ447933	AY786061	DQ059047
<i>Porothelium fimbriatum</i>	—	CBS 788.86	ag	DQ490626	DQ457673	DQ444854	DQ447907	DQ472721	—
<i>Pleurocybella porrigens</i>	—	JFA 12544 (WTU)/ TUB012154/ UPS F-611822	ag, pl	MT232355	MT232309	GU187660	DQ067994	MT24239	GU187740
<i>Pleurotus eryngii</i>	—	X102	ag, pl	KX977448	—	FJ379286	—	—	—
<i>P. ostreatus</i>	—	TENN 53662	—	NG_027634	AY645052	AY657015	AY862186	AY786062	AY883432
<i>Plicaturopsis crispa</i> *	—	FD-325 SS-3	ag, pl	genome	genome	genome	genome	genome	genome
<i>Podoserpula pusio</i>	—	Hlepp-329	ag	—	EF535271	—	—	—	—
<i>Porodaedalea pini</i>	—	No-6170-T	hy	JX110037	JX110081	—	—	JX109951	—

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Table 2. (Continued).

Original name	Updated name	Voucher specimen	Dataset	GenBank accession numbers					
				5.8S	28S	18S	RPB1	RPB2	EF-1 α
<i>Pseudoclitocybe cyathiformis</i>	—	JFA 12811 (WTU)/ GLM 46020 (GB)	ag	GU187553	EF551313	GU187659	DQ067939	GU187815	GU187742
<i>Pterulicium echo</i> (1)	—	DJM 302S58 (MINN)	ag, pl	DQ494693	AY458123	DQ092911	—	GU187805	GU187743
<i>P. echo</i> (2)	<i>cf. Pterula</i>	ZRL20151311	pl	LT716065	KY418881	KY418947	KY418979	KY419026	KY419076
<i>P. gracile</i> *(1)	—	CBS 309.79	ag, pl	genome	genome	genome	genome	genome	genome
<i>P. gracile</i> (2)	—	IO.14.142 (S)	pl	MT232356	MT232310	MT232498	—	—	MT242358
<i>Radulomyces confluens</i> *	—	OMC1631	ag, pl	genome	genome	genome	genome	genome	genome
<i>R. molaris</i>	—	ARAN-Fungi 2003	ag, pl	—	MT232311	MT232499	MT24230	MT24230	MT242359
<i>Ramariopsis biformis</i>	—	JMB10061006 (TENN065660)	cl	—	HQ877712	—	—	—	—
<i>R. crocea</i>	—	JMB10071001 (TENN065661)	cl	—	HQ877715	—	—	—	—
<i>R. aff. kunzei</i>	—	Marr5064 (WTU)	cl	—	HQ877719	—	—	—	—
<i>R. pseudosubtilis</i>	—	RHP27722 (TENN027722)	cl	—	HQ877723	—	—	—	—
<i>R. tenuiramosa</i>	—	GG_061104	cl	—	EF535269	—	—	—	—
<i>Repetobasidium conicum</i>	—	KHL 12338 (GB)	hy	DQ873647	DQ873647	DQ873646	—	—	—
<i>R. mirificum</i>	—	FP-133558-sp	hy	—	AY293208	AY293155	—	—	—
<i>Resinicium bicolor</i>	—	GEL 2071 (KASSEL)	hy	DQ218310	AY700183	—	—	DQ457635	—
<i>Rickenella fibula</i>	—	PBM 2503 (WTU)	hy	DQ241782	AY700195	AY771599	—	DQ408115	—
<i>Rhodocollybia maculata</i>	—	WTU	ag	DQ404383	AY639880	AY752966	DQ447936	AY787220	DQ061279
<i>Sarcomyxa serotina</i>	—	WTU/ DSH 93-218	ag, pl	DQ494695	AY691887	AF026590	DQ447938	DQ859892	GU187754
<i>Schizophyllum radiatum</i>	—	FH	ag	AY571060	AY571023	AY705952	DQ447939	DQ484052	—
<i>Schizopora radula</i>	—	Dai 12631	hy	KT203307	KT203328	—	—	KT210382	—
<i>Sclerotium complanatum</i>	<i>Macrotyphula phacorrhiza</i>	<i>Microf. Exs. No. 49</i> (UPS)	pl	—	MT234400	—	—	—	—
<i>Sistotrema confluens</i>	—	FCUG 298	hy	DQ267125	AY647214	AY757260	—	DQ381837	—
<i>Stephanospora caroticolor</i>	—	TUB019072/ IOC 137-97/ R44008	ag, pl	KM086827	AF518652	AF518591	KF211335	—	GU187747
<i>Trichaptum abietinum</i> *	—	R44008	hy	genome	genome	genome	—	genome	—
<i>Tubulicrinis globisporus</i>	—	KHL 12133 (GB)	hy	DQ873655	DQ873655	DQ873654	—	—	—
<i>T. inomatus</i>	—	KHL 11763 (GB)	hy	DQ873659	DQ873659	DQ873658	—	—	—
<i>Tygervalleyomyces podocarpi</i>	<i>Typhula podocarpi</i>	CPC 29979		NR_156661	NG_059851	—	—	—	—
<i>Typhula capitata</i>	—	IO.15.122 (S, UPS)/ CBS 143727	ag, pl	MT232357	MT232312	MT232500	MT24231	MT24231	MT242360
<i>T. crassipes</i>	—	IO.14.83 (S, UPS)	ag, pl	MT232358	KY224094	—	—	MT24232	MT242361
<i>T. erythropus</i>	—	IO.14.123 (S, UPS)/ CBS 143797	ag, pl	MT232359	KY224096	MT232501	MT24232	MT24233	MT242362
<i>T. gyrans</i>	—	IO.14.103 (S)/ CBS 143796	ag, pl	MT232360	KY224097	MT232502	MT24233	MT24234	MT242363

Table 2. (Continued).

Original name	Updated name	Voucher specimen	Dataset	GenBank accession numbers					
				5.8S	28S	18S	RPB1	RPB2	EF-1 α
<i>T. micans</i>	—	IO.14.165 (S)	ag, pl	MT232361	KY224102	MT232503	MT24234	MT24235	MT242364
<i>T. incarnata</i>	—	IO. 14. 92 (S)/ CBS 143742/ CBS 350.79	ag, pl	MT232362	MT232313	MT232504	MT24235	MT24236	MT242365
<i>T. phacorrhiza</i> (1)	<i>Macrotyphula phacorrhiza</i>	IO.14.200 (S)	ag, pl	MT232363	MT232314	MT232505	—	MT24237	MT242366
<i>T. phacorrhiza</i> (2)	<i>M. phacorrhiza</i>	IO.14.167 (S)	ag, pl	MT232364	MT232315	MT232506	MT24236	MT24238	MT242367
<i>T. phacorrhiza</i> (3)	<i>M. juncea s.l.</i>	DSH 96-059	pl	—	AF393079	AF026630	—	AY218525	—
<i>T. phacorrhiza</i> (4)	<i>M. phacorrhiza</i>	ARAN-Fungi 7446	pl	—	MT232316	—	—	—	MT242368
<i>T. sclerotoides</i>	—	IO.14.22 (S)	ag, pl	MT232365	MT232317	MT232507	MT24237	MT24239	MT242369
<i>T. subhyalina</i>	—	IO.15.06 (S)/ CBS 143735	ag, pl	MT232366	MT232318	MT232508	—	MT24230	MT242370
<i>T. uncialis</i>	—	IO.14.74 (S)	ag, pl	MT232367	MT232319	MT232509	MT24238	MT24231	MT242371
Uncultured <i>Basidiomycota</i> (5)	<i>Ceratellopsis</i> sp.	Soil sample	cl	DQ341741	DQ341741	—	—	—	—
Uncultured <i>Basidiomycota</i> (1)	<i>Ceratellopsis</i> sp.	Soil sample	cl	HQ433218	HQ433218	—	—	—	—
Uncultured <i>Basidiomycota</i> (2)	<i>Ceratellopsis</i> sp.	Soil sample	cl	GQ159941	GQ159941	—	—	—	—
Uncultured <i>Basidiomycota</i> (3)	<i>Ceratellopsis</i> sp.	Soil sample	cl	EU691875	EU691875	—	—	—	—
Uncultured <i>Basidiomycota</i> (4)	<i>Ceratellopsis</i> sp.	Soil sample	cl	EU861817	EU861817	—	—	—	—
Uncultured <i>Basidiomycota</i> (5)	<i>Ceratellopsis</i> sp.	Soil sample	cl	DQ341741	DQ341741	—	—	—	—
Uncultured <i>Basidiomycota</i> (6)	<i>Ceratellopsis</i> sp.	Soil sample	cl	EF434117	EF434117	—	—	—	—
Uncultured <i>Basidiomycota</i> (7)	<i>Ceratellopsis</i> sp.	Soil sample	cl	GQ159939	GQ159939	—	—	—	—
<i>Xerula radicata</i>	—	TENN 59235	ag	DQ241780	AY645051	AY654884	DQ447946	AY786067	DQ029194
<i>Xylodon rimosissimus</i>	—	CBS 105.045/ Ryberg 021031 (GB)	hy	DQ873627	DQ873628	DQ873626	—	LN714662	—

and closely related families, with a more species-inclusive sampling than in the *Agaricales* matrix. *Cantharocybe gruberi* was used as an outgroup based on analyses of the *Agaricales* matrix. A third 28S alignment (the *Clavariaceae* matrix) was constructed based

on Birkebak *et al.* (2013) to infer phylogenetic relationships of *Ceratellopsis* within the *Clavariaceae*, and employed *Anomoporia bombycina*, *A. kamschatica* and *Podoserpula pusio* as outgroup taxa. A fourth 4-locus (5.8S, 28S, 18S, *RPB2*) dataset (the

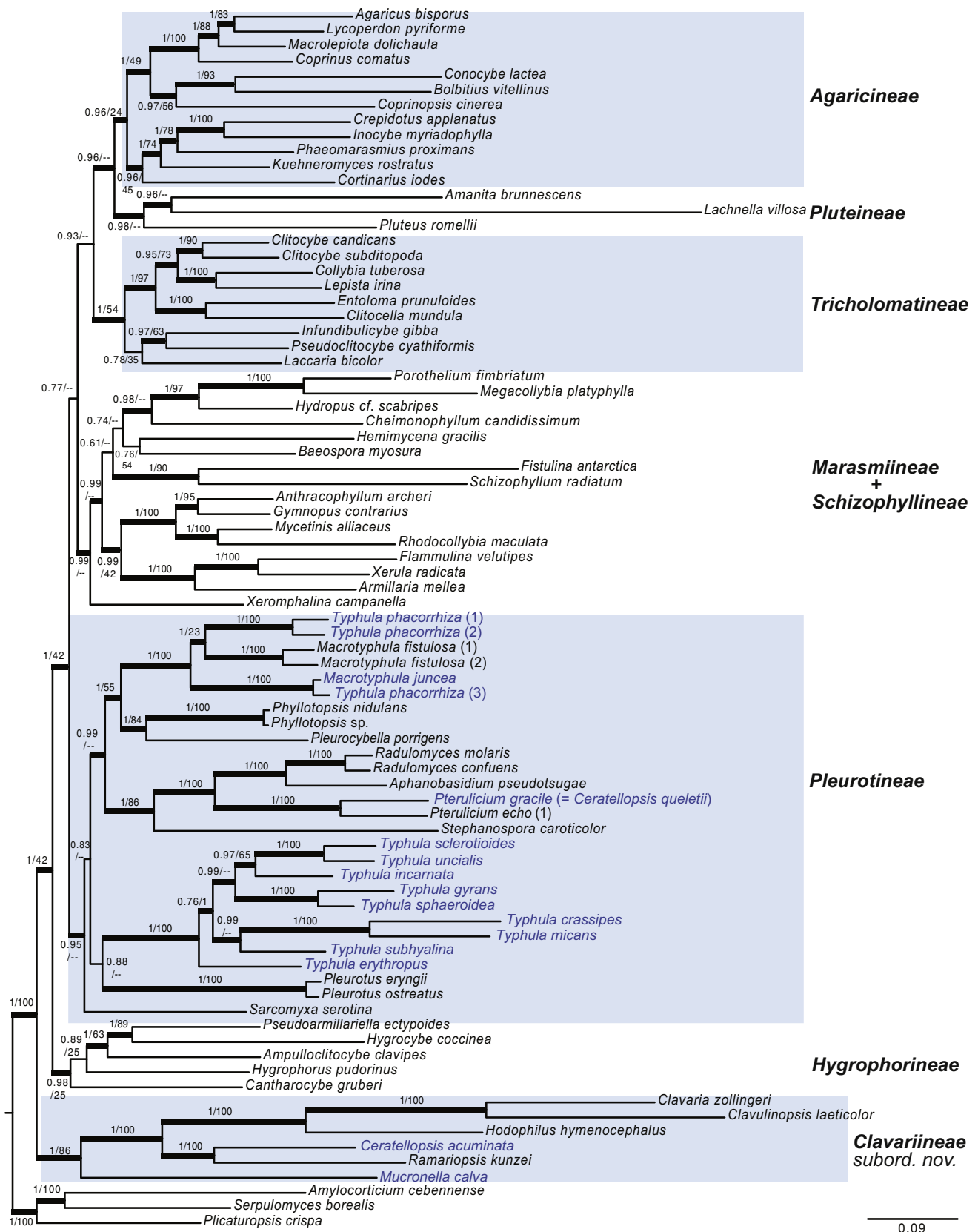


Fig. 2. Bayesian inference 50 % majority rule consensus phylogram of the *Agaricales* from 5.8S-18S-28S-*RPB1*-*RPB2*-*EF-1 α* sequence data, with the placement of typhuloid fungi (in blue font). Bayesian posterior probabilities (PP) and Maximum Likelihood bootstrap values (ML-BP) are shown on branches, ordered as PP/ML-BP. Thickened branches received support at least in one analysis (ML-BP \geq 70 % and/or PP \geq 95 %). Suborder names recognised within the *Agaricomycetes* are indicated on the right side.

Hymenochaetales matrix) was assembled to further explore phylogenetic relationships of *C. sagittiformis* within the *Hymenochaetales*. Sequences of *Calocera cornea* were set as outgroup.

Sequence alignment and phylogenetic analyses

Sequences were edited and assembled using Sequencher v. 4.10.1 (Gene Codes Corp., Ann Arbor, MI) and deposited in GenBank (Table 2). Additional sequences were downloaded

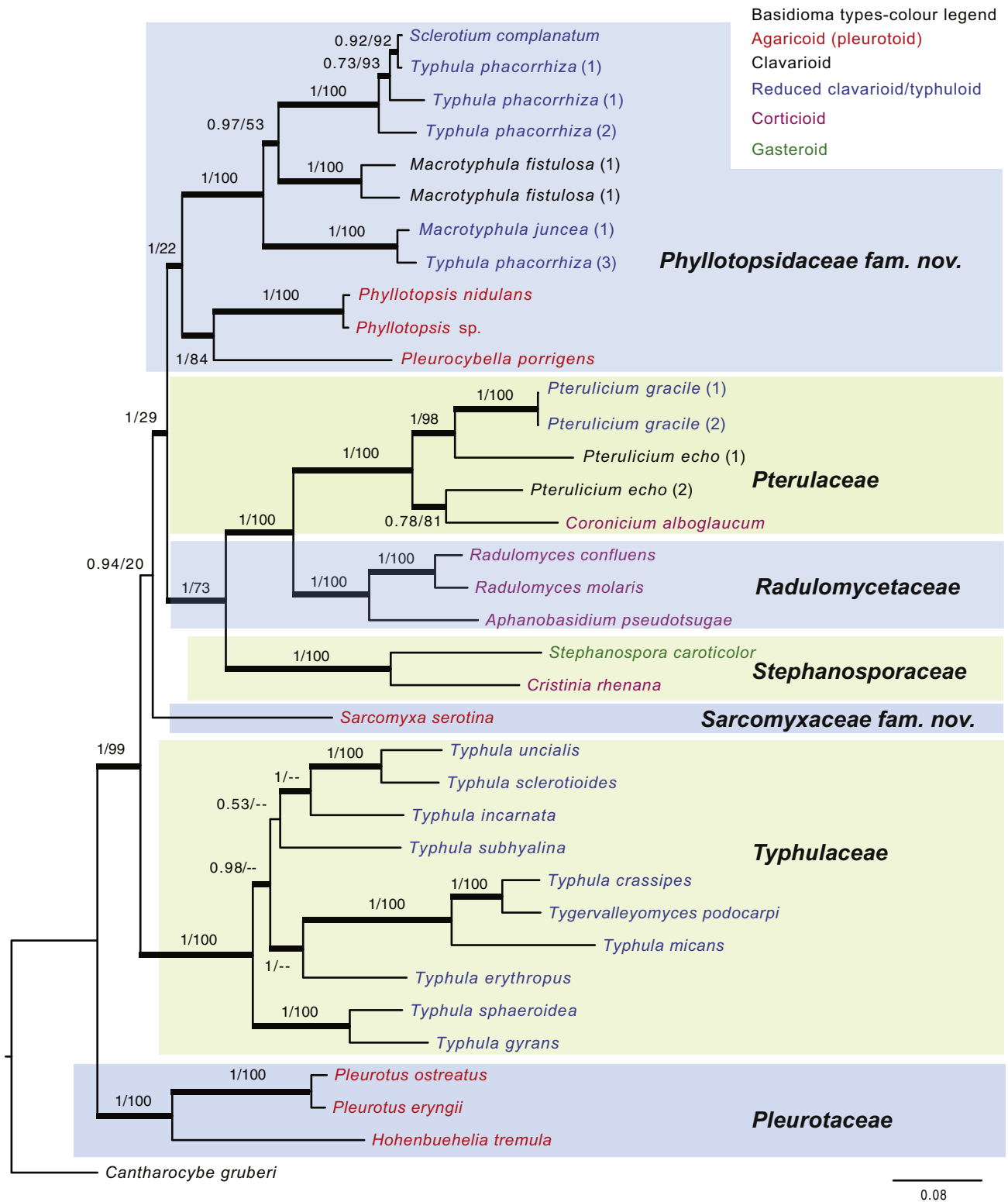


Fig. 3. Bayesian inference 50 % majority rule consensus phylogram of the *Pleurotineae* from 5.8S-18S-28S-RPB1-RPB2-EF-1 α sequence data. Bayesian posterior probabilities (PP) and Maximum Likelihood bootstrap values (ML-BP) are shown on branches, ordered as PP/ML-BP. Thickened branches received support at least in one of the analyses (ML-BP \geq 70 % and/or PP \geq 95 %). Family names recognised within the *Pleurotineae* are marked with colour boxes. Basidioma types are indicated with different colours for ingroup taxa.

from GenBank and from the following genomes through the MycoCosm portal (Grigoriev et al. 2014): *Agaricus bisporus*, *Coprinopsis cinerea* (Muraguchi et al. 2015), *Laccaria bicolor* (Martin et al. 2008), *Onnia scaura*, *Phellinus ferrugineofuscus*, *Plicaturopsis crispa* (Kohler et al. 2015), *Pterulicium gracile* (Varga et al. 2019, deposited as *Pterula gracilis*), *Radulomyces confluens* and *Trichaptum abietinum* (Table 2). Nucleotide sequences were aligned manually using Aliview (Larsson 2014). Protein-coding genes were translated to amino acids to determine intron positions. In order to check gene-tree congruence, each individual gene-region was analysed using a ML approach, as explained above. Gene congruence was assessed manually by comparing supported clades among single-gene genealogies (Mason-Gamer & Kellogg 1996). Clades were considered in conflict if a supported clade (ML-BP >70 %) for one marker was contradicted with significant support by another one. Since no conflict was detected, markers were concatenated in the *Agaricales*, *Typhulaceae* and *Hymenochaetales* alignments. Introns were excluded and the third codon position was partitioned in the protein-coding genes (*RPB1*, *RPB2* and *EF-1 α*). Each matrix was subjected to ML and Bayesian analyses. ML analyses were conducted as explained above. Bayesian analyses were implemented in MrBayes v. 3.2.6 (Ronquist et al. 2012), using two parallel runs of eight Metropolis-coupled Markov chain Monte Carlo (MCMCMC) chains for 30 M generations, starting from a random tree, and sampling one tree every 1 000th generation from the posterior distribution. Substitution models were sampled across the GTR space during the MCMC simulation (Ronquist et al. 2012). Stationarity was assumed when average standard deviation of split frequencies fell below 0.01. A burn-in sample of 30 000 trees was discarded. To assess branch confidence, a 50 % majority rule consensus tree was computed with the remaining 30 002 trees using the SUMT command of MrBayes. Bayesian posterior probability (PP) values ≥ 0.95 were considered to be significant. The alignments and respective phylogenetic trees were deposited in TreeBASE, study number S25967.

RESULTS

Origins of typhuloid fungi within *Agaricales* and *Pleurotineae*

A total of 118 (21 5.8S, 23 28S, 18 18S, 13 *RPB1*, 23 *RPB2*, 20 *EF-1 α*) sequences were generated for this study (Table 2). The *Agaricales* matrix comprised 81 taxa and contained 6 292 unambiguously aligned nucleotide positions (161 nu5.8S, 1 480 nu28S, 1 745 nu18S, 861 *RPB1*, 1 056 *RPB2* and 989 *EF-1 α*), with all genes available for 86.4 % of taxa. The *Pleurotineae* matrix had 39 taxa and contained 6 215 unambiguously aligned nucleotide positions (159 nu5.8S, 1 418 nu28S, 1 732 nu18S, 863 *RPB1*, 1 056 *RPB2* and 987 *EF-1 α*), with all genes available for 72.2 % of taxa. The Bayesian analysis of the *Agaricales* and *Pleurotineae* datasets reached average standard deviations of split frequencies > 0.01 after 12 195 000 and 425 000 generations, respectively. The Bayesian majority rule consensus tree of the *Agaricales* was fully resolved and many deeper branches received high support by Bayesian PP (Fig. 2). The majority of these branches were, however, not supported by ML-BP (< 70 %). Typhuloid fungi do not form a monophyletic group.

Specimens with skeletal hyphae nest in *Pleurotineae* (*Pterulicium gracile*) and in *Clavariineae* (*C. acuminata*). Sequences of the specimen of *P. gracile* collected by us (IO.14.142) were identical to those obtained from the available genome of *P. gracile* (CBS 309.79) (Fig. 3), employed also by Leal-Dutra et al. (2020). *Clavariineae* forms a strongly supported clade (PP 1, ML-BP 86) that is resolved as an early diverging lineage within *Agaricales* (PP 1). *Ceratellopsis acuminata* forms a highly supported clade with *Ramariopsis kunzei* (PP 1, ML-BP 100). The remaining *Agaricales* form a strongly supported monophyletic group (PP 1), within which *Ampulloclitocybe clavipes*, *Cantharocybe gruberi*, *Hygrocybe coccinea*, *Hygrophorus pudorinus* and *Pseudoarmillariella ectypoides*, corresponding to the *Hygrophoraceae*, constitute a strongly supported lineage in the Bayesian analysis (PP 0.98), as a sister group to the rest of the *Agaricales* (PP 1). The suborders *Agaricineae* (PP 0.96), the *Tricholomatineae* (PP 1), the *Marasmiineae* (PP 0.99) and the *Pluteineae* (PP 0.95) also received high support in the Bayesian analysis. *Xeromphalina campanella*, previously assigned to the hygrophoroid clade, is supported as an early diverging sister lineage to the *Marasmiineae* (PP 0.99). Species of *Typhula* and *Macrotyphula* form a well-supported clade together with other pleurotoid, clavarioid, corticioid and gasteroid species (PP 0.95) that is referred to the *Pleurotineae*. The *Agaricales* (ag) and *Pleurotineae* (pl) phylogenies (Figs 2, 3) show similar supported nodes in the *Pleurotineae*, except that the *Pleurotaceae* formed a sister group to the rest of the *Pleurotineae* in both Bayesian and ML analyses of the *Pleurotineae* matrix (PP 1, ML-BP 99). In all analyses *T. phacorrhiza* is nested within a monophyletic *Macrotyphula* (ag PP 1, ML-BP 100; pl PP 1, ML-BP 100). A specimen identified as *Sclerotium complanatum* is nested within a clade of three *T. phacorrhiza* collections in the analyses of the *Pleurotineae* matrix. The *Macrotyphula* clade is encompassed in a larger supported clade together with *Phyllotopsis* and *Pleurocybella porrigens* (pl PP 1). *Stephanospora caroticolor*, *Cristinia rhenana*, *Pterulaceae* and *Radulomycetaceae* (*Aphanobasidium*, *Radulomyces*) form a strongly supported clade (pl PP 1, ML-BP 73) sister to the *Macrotyphula* clade, *Phyllotopsis* and *Pleurocybella porrigens*. All *Typhula* species but its type *T. phacorrhiza*, form a distinct separate lineage (pl PP 1, ML-BP 100). It includes the types of *Cnazonaria*, *Dacryopsella*, *Gliocoryne*, *Phacorrhiza*, *Pistillaria*, *Pistillina*, *Scleromitra*, *Sphaerula* and *Tygeralleyomyces*. *Typhula* is a sistergroup to the clade formed by *Macrotyphula*, *Phyllotopsis*, *Pleurocybella porrigens*, *Pterulaceae* and *Stephanosporaceae* in the *Pleurotineae* phylogeny (Fig. 3), albeit without support (pl PP 0.94). *Pleurotus* and *Hohenbuehelia tremula* are supported as a sistergroup to the rest of the *Pleurotineae* in the *Pleurotineae* phylogeny (Fig. 3, PP 1, ML-BP 99).

The *Clavariaceae* phylogeny

The *Clavariaceae* matrix comprised 53 taxa and contained 1 505 unambiguously aligned nucleotide positions (28S rDNA). Bayesian and ML analyses produced very similar topologies (Fig. 4). Species of *Mucronella* form a highly supported sister group to the rest of the *Clavariaceae* (PP 1, ML-BP 100). *Clavaria*, *Camarophyllopsis*, *Hodophilus* and *Hirticlavula elegans* form a highly supported monophyletic group (PP 1, ML-BP 84), characterised by lacking clamp connections on context hyphae in all species but *Clavicornia taxophila*. Three species of

Ceratellopsis form a distinct clade with several environmental sequences (uncultured *Basidiomycota* in GenBank). The relationships of the *Ceratellopsis* clade to the other genera with clamp connections, *Ramariopsis* and *Clavulinopsis*, are not resolved with support.

The Hymenochaetales phylogeny

The *Hymenochaetales* matrix contained 37 taxa and 4 239 unambiguously aligned characters. The majority rule consensus tree of the Bayesian analysis is provided in Fig. 5. The *Hymenochaetales* is recovered as monophyletic with

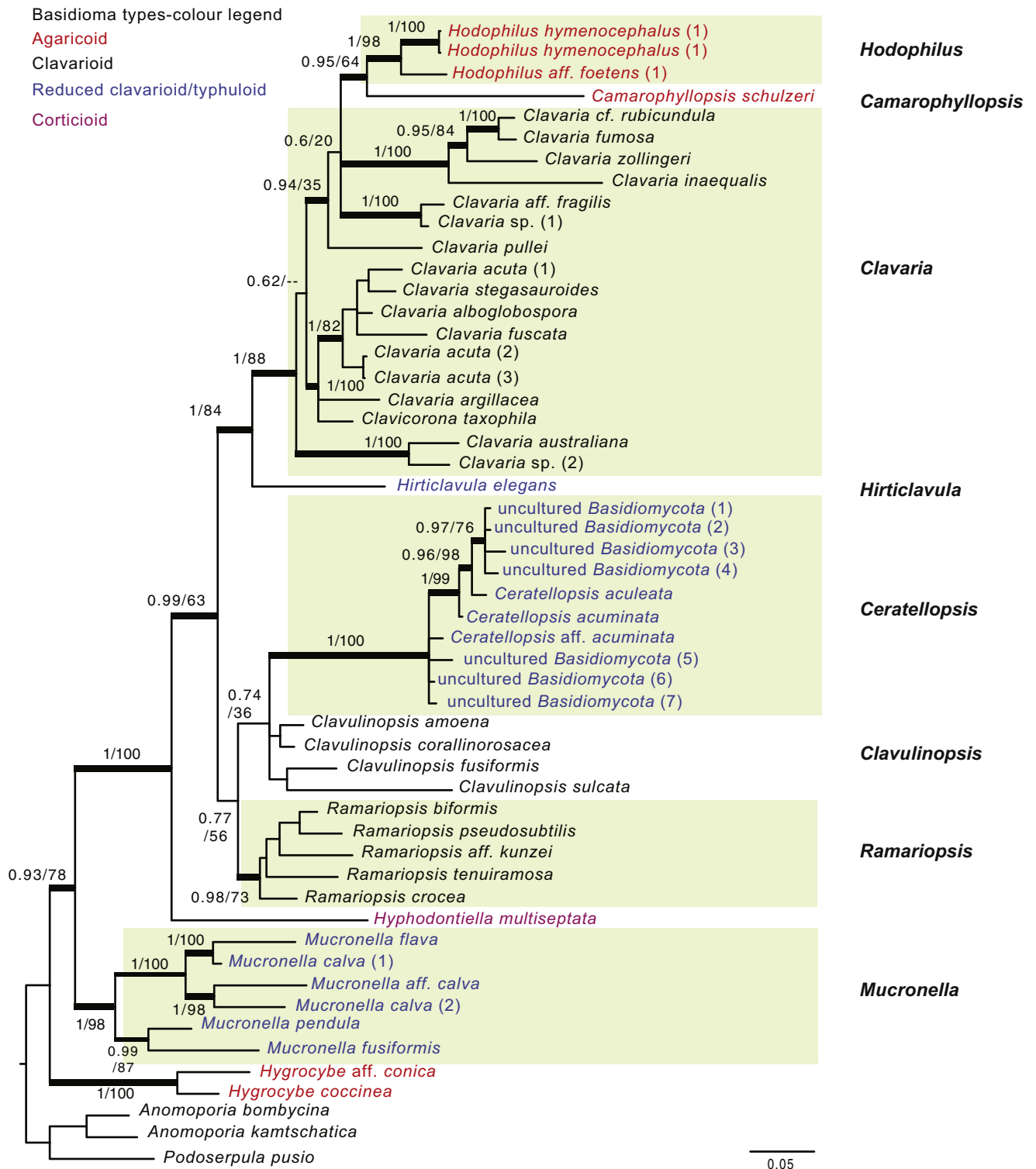


Fig. 4. Bayesian inference 50 % majority rule consensus phylogram of the *Clavariineae* from 28S sequence data. Bayesian posterior probabilities (PP) and Maximum Likelihood bootstrap values (ML-BP) are shown on branches, ordered as PP/ML-BP. Thickened branches received support at least in one analysis (ML-BP ≥ 70 % and/or PP ≥ 95 %). Basidioma types are indicated with different colours for ingroup taxa.

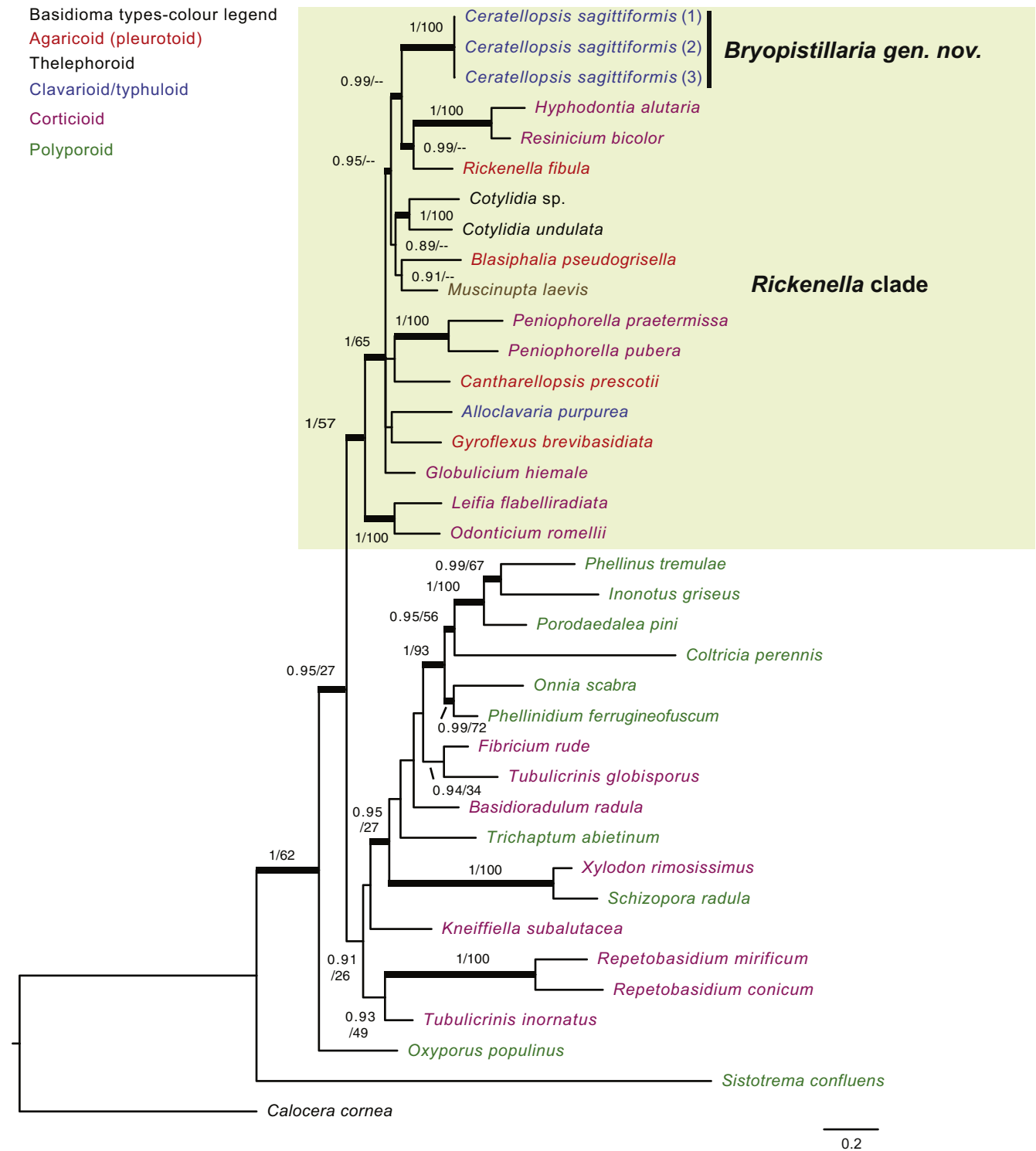


Fig. 5. Bayesian inference 50 % majority rule consensus phylogram of the hymenochaetoid clade from 5.8S-18S-28S-RPB2 sequence data. Bayesian posterior probabilities (PP) and Maximum Likelihood bootstrap values (ML-BP) are shown on branches, ordered as PP/ML-BP. Thickened branches received support at least in one analysis (ML-BP ≥ 70 % and/or PP ≥ 95 %). Basidioma types are indicated with different colours for ingroup taxa.

high support in the Bayesian analysis (PP 1, ML-BP 62). It comprises two larger clades: a) a clade containing *Coltricia*, *Kneiffiella*, *Xylodon* and *Hymenochaetaceae*, corresponding to clades C–F in Larsson *et al.* (2006), along with two species of *Repetobasidium* (PP 0.91, ML-BP 26); and b) a clade corresponding to the *Rickenella* clade (clade B in Larsson *et al.* 2006) (PP 1, ML-BP 57). Within the *Rickenella* clade, the three *Ceratellopsis sagittiformis* specimens are encompassed in a well-supported clade (PP 1, ML-BP 65) with species of

agaricoid (*Blasiphalia*, *Cantharellopsis*, *Gyroflexus*, *Rickenella*), clavarioid (*Alloclavaria*), corticioid (*Globulicium*, *Hyphodontia*, *Peniophorella*, *Resinicium*), cyphelloid (*Muscinupta*) and thelephoroid (*Cotylidia*) basidiomata. The position of *Hyphodontia alutaria* and *Resinicium bicolor* is in conflict; both species form a supported monophyletic group with *Rickenella fibula* and *C. sagittiformis* in the Bayesian analysis (PP 99), as opposed to a monophyletic group with *Cotylidia* spp. in the ML analysis (ML-BP 75).

Taxonomy

Clavariineae Olariaga, Huhtinen, Læssøe, J.H. Petersen & K. Hansen, **subord. nov.** MycoBank MB831365.

Basidiomata clavarioid, more rarely agaricoid with waxy decurrent gills, or corticioid. Hyphal system monomitic, or more rarely dimitic. *Basidiospores* hyaline, usually thin-walled, smooth or ornamented, usually with multiguttulate contents, sometimes with amyloid or dextrinoid reactions, usually with a cubic apiculus. *Basidia* claviform, with up to 4 sterigmata, chiasitic, sometimes characteristically long (< 50 µm) or short (> 20 µm), occasionally sometimes with a loop-like basal clamp (*Clavaria* subgen. *Holocoryne*). *Cystidia* usually absent. *Pileipellis* either a hymeniderm or a trichoderm with rounded terminal elements in genera with agaricoid basidiomata. *Basal tomentum* composed of narrow, usually < 2 µm broad thick-walled hyphae in clavarioid genera

(*Ceratellopsis*, *Clavaria*, *Clavulinopsis*, *Ramariopsis*), possibly also in other stipitate genera. *Clamp connections* present or absent, sometimes restricted to basidia. Saprotrophic on dead wood, herbaceous plants or leaves, or biotrophic with grasses and bryophytes. Presence of *EF-1α* intron 21 (numbering according to Matheny *et al.* 2007) in some genera (absent in *Ceratellopsis*).

Type family: Clavariaceae Chevall.

Notes: This suborder contains a single family. Similar isotopic ratios to those found in the *Hygrophoraceae* suggest that at least non-lignicolous members of *Clavariaceae* have some kind of biotrophic association with plants (Birkebak *et al.* 2013), whereas genera occurring on dead plant remnants are probably saprotrophic (*Ceratellopsis*, *Mucronella*, *Hirticlavula*). Very narrow and slightly thick-walled hyphae in the basal tomentum and mycelium

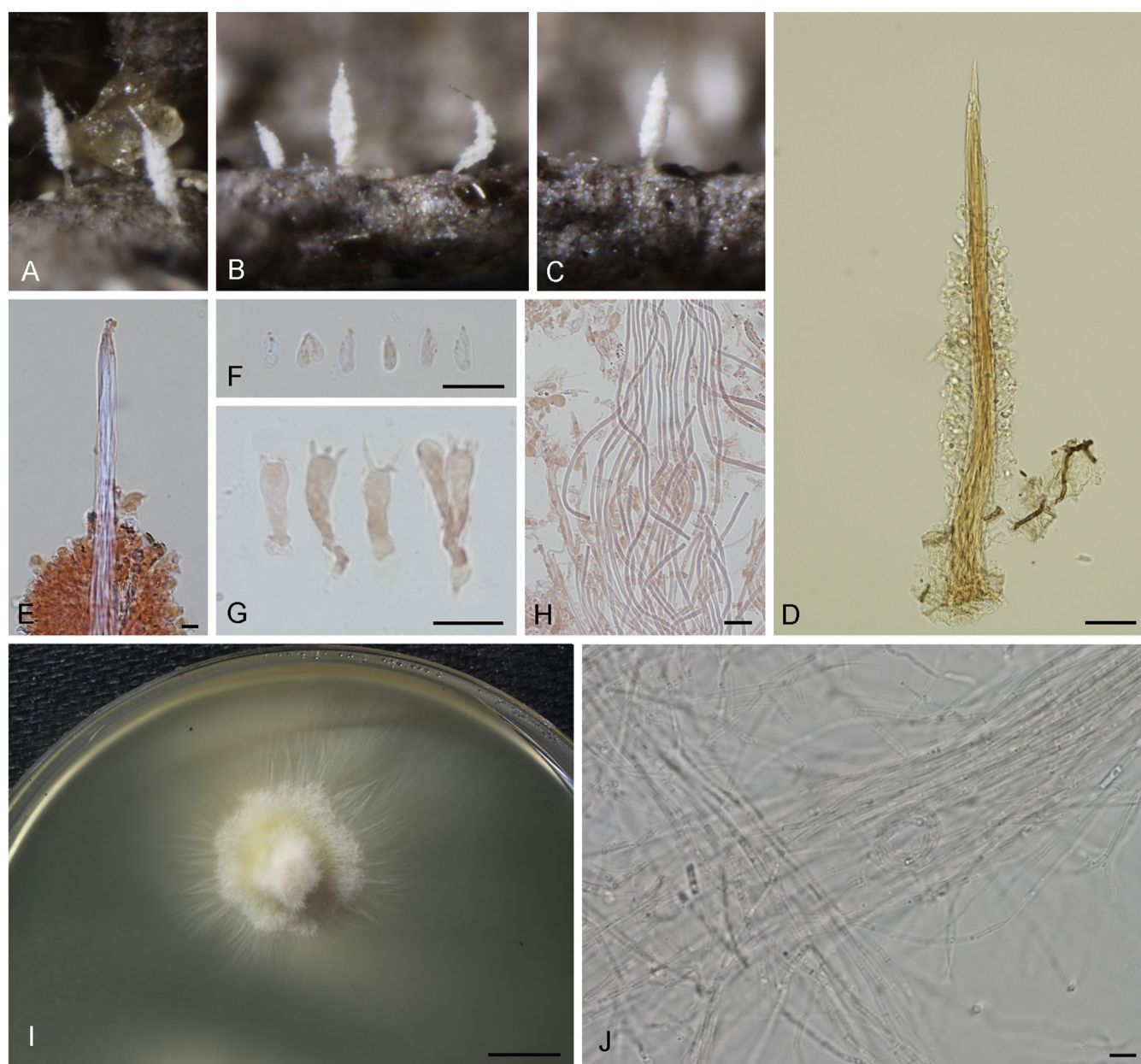


Fig. 6. *Ceratellopsis acuminata* (epitype, Huhtinen 15/07, S). **A–C.** Dried basidiomata. **D.** Basidioma observed using a light microscope. **E.** Close-up of basidioma apex. **F.** Basidiospores. **G.** Basidia. **H.** Medullar hyphae resembling skeletal hyphae. **I.** One-year-old culture in MEA, kept at 5 °C (culture ex-epitype, CBS 146691). **J.** Hyphae from cultured mycelium (culture ex-epitype, CBS 146691). Mounting media were Melzer's reagent (D), Congo Red in ammonia (E–H) and water (I). Scale bars: D = 100 µm, E–H = 10 µm; I = 10mm. Photographs I. Olariaga.

are characteristic for many species of *Clavariaceae*, including species in *Clavaria*, *Clavulinopsis*, *Ramariopsis* (Olariaga 2009) and *Ceratellopsis* (Fig. 6) and it might be a synapomorphic character of the *Clavariineae*. The presence of *EF-1 α* intron 21, absent in the rest of the *Agaricales* (Matheny et al. 2007) seems so far unique to some *Clavariaceae* (*Clavaria*, *Clavulinopsis*, *Camarophyllopsis*).

Clavariaceae Chevall., Fl. Gen. Env. Paris 1: 102. 1826. ["Clavariae"; "ordre"; considered family according to Art. 18.2].

Type genus: *Clavaria* Vaill. ex L.: Fr.

Genera: *Camarophyllopsis*, *Ceratellopsis*, *Clavaria*, *Clavulinopsis*, *Hirticlavula*, *Hodophilus*, *Hyphodontiella*, *Mucronella*, *Ramariopsis*.

Ceratellopsis Konrad & Maubl., Icon. Select. Fung. 6: 502. 1937.

Basionym: *Ceratella* Pat., Hymenomyc. Eur.: 137. 1887. [nom. illeg. Art. 53.1, later homonym of *Ceratella* Hook f. 1844].

Presumed saprobic on bark, dead wood or culms. *Basidiomata* gregarious, clavarioid, 0.2–1(–2) mm high, lanceolate with a sterile pointed apex, white. Stipe usually present, short, glabrous or pubescent. Hyphal system monomitic or dimitic. *Basidiospores* without iodine reactions. *Basidia* claviform, short, 10–16 μ m long. *Generative hyphae* present in the medulla, unidirectional, cylindrical, septate, thick-walled, 1–2.5 μ m broad, sometimes dextrinoid. *Skeletal hyphae* present in the medulla of *C. acuminata* and further undescribed species known by us. *Clamp connections* scattered.

Type: *Ceratellopsis acuminata* (Fuckel) Corner, typ. cons. prop.

Notes: The background of the name *Ceratellopsis* requires, however, further clarification as its type has been a matter of controversy. According to our nomenclatural study, *Ceratellopsis* is a validly published replacement name based on *Ceratella* Pat. and typified by *Pistillaria queletii*. The final epithet *Ceratella* was first employed by Quélet (1886) for an unranked infrageneric name. Later, although Patouillard (1887) referred to *Ceratella* as "CERATELLA (Quélet)" he did not have in mind *Clavaria* [unranked] *Ceratella* as the basionym of a new combination. As explained in the introduction of the Hymenomycetes (Patouillard 1887: VII), authors of generic names were cited between round brackets only when Patouillard's circumscriptions were absolutely different from the original ones. Therefore, we consider *Ceratella* as the name of a new taxon to be cited as "*Ceratella* Pat." (J. McNeill, pers. comm.) in agreement with Donk (1954) and the ING (Farr & Zijlstra 2020). Nevertheless, *Ceratella* Pat. (1887) is illegitimate as a later homonym of *Ceratella* Hook f. (1846). When *Ceratellopsis* was introduced, Konrad & Maublanc (1937) referred to it as a new name for "*Ceratella* (Quélet p.p.), Patouillard (1887)" and proposed *Ceratellopsis queletii* as the type, without providing a Latin description. Since *Ceratellopsis* was a replacement name for *Ceratella* Pat., and not a new taxon, *Ceratellopsis* is a validly published generic name even though it lacked a Latin description and was published later than 1935 (Art. 39.1), because such is not required for a replacement name. The type proposed for *Ceratellopsis* by Konrad & Maublanc is also in order, since *Ceratella queletii* was one of the three species listed under *Ceratella* Pat. (1887). A relevant fact that might have affected the typification of *Ceratellopsis* is whether the combination *Ceratella queletii* was validly published when Patouillard

erected *Ceratella* Pat. Patouillard (1887) listed *C. queletii* as "*C. Queletii*" without explicitly citing its basionym *Pistillaria queletii*. However, we interpret that Patouillard (1887: VI) gave an indirect reference to the basionym that fulfils conditions for valid publication of *C. queletii* (Art. 41.3 and 38.14) by explicitly stating that *Tabulae Analyticae Fungorum*, the place of publication of *Pistillaria queletii*, basionym *C. queletii*, was one of the main works on which he based his Hymenomycetes (Art. 41.4, Ex. 9), and because Patouillard himself was author of the basionym.

For details on our choice to suggest *C. acuminata* as the conserved type for *Ceratellopsis* see notes under *Pterulicium* and the Discussion.

Ceratellopsis acuminata (Fuckel) Corner, Ann. Bot. Mem. 1: 202. 1950. Fig. 6.

Basionym: *Pistillaria acuminata* Fuckel, Fungi Rhen. Exs. (suppl.) 4: no 1888. 1867.

Synonym: *Ceratella acuminata* (Fuckel) Pat., Essai Tax. Hymenomyc.: 49. 1900.

Basidiomata gregarious, 0.2–0.4 mm high, simple, with a short stipe and a sterile apex. Fertile part cylindrical to oblong, sharply delimited from the stipe and the apex, white, 0.1–0.3 \times 0.02–0.04 mm. Stipe short, cylindrical, glabrous, hyaline white, 0.04–0.12 \times 0.01–0.02 mm. Apex pointed, acute, hyaline white, 0.04–0.1 mm long. *Basidiospores* ellipsoid to pip-shaped, sometimes in tetrads, hyaline, without iodine reactions, (3–) 4–6 \times (1.5–) 2–3 μ m. *Basidia* claviform, 2–4-spored, 10–16 \times 3.5–4.5 μ m, clamped. *Generative hyphae* cylindrical, hyaline, thin-walled, clampless, sometimes with scarce septa at the stipe base, 1–2.2 μ m broad. *Skeletal hyphae* present in the medulla, cylindrical, refractive, slightly dextrinoid, 1.2–2.8 μ m broad. Colonies on MEA 30–40 mm diam after 1 yr at 5 °C, superficial, effuse, convex, tomentose, hard-textured, with erect white tufts and strong smell reminiscent of *Scleroderma*. Reverse white. Margin regular and distinct. Vegetative hyphae cylindrical, closely septate, very slightly thick-walled, hyaline, 2.5–4 μ m broad, with scattered clamp connections. Asexual morph not observed in culture.

Typus: Germany, Nassau, Johannisberger Schlosswald, ad pini sylv. folia putrida falae humus, Fuckel, Fungi Rhen. Exs. no 1888 (S-F128455 !, lectotype of *Pistillaria acuminata* designated here, MycoBank MBT387677). Isolectotypes: S-F128454 (!), S-F267533 (!), FH00608504 (!), K(M) 159801, M. Sweden, Härjedalen, Tännadalen, Hamrafjället Nature Protection Area, on dead leaves of *Dryas octopetala*, 4 Aug. 2015, S. Huhtinen 15/07 (S, epitype of *Pistillaria acuminata* designated here, MycoBank MBT389356). Culture ex-epitype: CBS 146691.

Known distribution: Denmark, Finland, France, Germany, Norway, Spain and Sweden.

Additional materials examined: Denmark, Sjælland, Bognæs skov, on leaves of *Leymus* on exposed beach, 26 Oct. 2019, T. Læssøe, DMS-10058526 (C). Finland, Perä-Pohjanmaa, Rovaniemi, Lovevaara Nature Protection area, brookside herb-rich forest, on leaf litter under alders, 7 Sep. 2012, S. Huhtinen 12/15 (TUR 197690). France, Val-d'Oise, Montmorency, ad cortices, 1889, Boudier herbarium (PC). Norway, Finnmark, Nord Varanger, Varanger Peninsula, Fosefjellet (ca. 3 km NW of Vadsø), on hare dung (*Lepus timidus*) in moist chamber, 27 Jul. 1966, N. Lundqvist 4965g (UPS F-152857). Sweden, Gästrikland, Gävle, Lövudden, *Salix viminalis*, folia dejecta, 25 Jun. 1953, J.A. Nannfeldt 12806 (UPS F-152650, as *Ceratellopsis* sp.); Lycksele Lappmark, Saxnäs, Satsfjället, on dead fern stems, 28 Jul. 2010, K. Hansen, K. Gillen & I. Olariaga, IO.10.01 (S); Västergötland, Håkantorps, Åspås hållplats, on *Quercus robur* leaves, 2 Oct. 1955, S. Kilander (UPS F-152830).

Notes: *Ceratellopsis acuminata* differs from *C. aculeata* in having skeletal hyphae in the basidioma core. Another collection identified as *C. aff. acuminata* by us (ARAN-Fungi 11746) possessed also skeletal hyphae, but had longer and shorter basidiomata and nested in a different clade than the epitype of *C. acuminata* (Fig. 4). This substantiates the idea that an additional species of *Ceratellopsis* exists and when more specimens become available the species limits should be studied further.

Corner (1950: 203) mentioned a type collection of *Pistillaria acuminata* (that Donk had examined in ms) without providing a collection number or a herbarium. Since we believe that Corner's type indication did not fulfil requirements for achieving a valid typification (Art. 7.11), we propose here a lectotypification of *C. acuminata*. The four syntypes examined are very meagre. Therefore, we select as epitype a recent collection from which a living culture and several gene regions have been obtained. We found *C. acuminata* to have a very broad host range and distribution, and feel justified in selecting Swedish material collected on *Dryas* leaves as epitype.

Ceratellopsis aculeata (Pat.) Corner, Ann. Bot. Mem. 1: 200. 1950.

Basionym: *Pistillaria aculeata* Pat., Tab. anal. Fung. 1: 26. 1883.
Synonyms: *Ceratelya aculeata* Pat., Essai Tax. Hyménomyc.: 49. 1900.

(?) *Pistillaria mucedinea* Boud., Bull. Soc. bot. Fr. 24: 308. 1878. [1877].

(?) *Ceratellopsis mucedinea* (Boud.) Corner, Ann. Bot. Mem. 1: 204. 1950.

Typus: No type specimen in the Patouillard herbarium (FH, PC).

Lectotype of *Pistillaria aculeata* designated here: Patouillard, Tab. Anal. Fung. 1: fig. 58. 1883. MycoBank MBT387467.

Specimens examined: **Denmark**, Lolland, Maribo Sønder, on stems of *Cladium mariscus*, 9 Oct. 2000, T. Læssøe, DMS-376001 (C). **Spain**, Aragón, Huesca, on *Pinus* bark, 26 Feb. 2017, R. Blasco, ARAN-Fungi 13729; Basque Country, Gipuzkoa, Larraul, Usarroi erreka, 9 Jun. 2012, I. Olariaga, ARAN-Fungi A3064020. **Sweden**, Öland, Norra Mosse, on damp, dead parts of *Cladium*, 2 Jul. 1988, S. Elborne, C-F-94548. **UK**, England, Wicken fen, on *Cladium mariscus*, 12 Aug. 1926, E.J.H. Corner (PC).

Notes: Medulla hyphae in *Ceratellopsis aculeata* are thick-walled and have scarce septa, as noted by Corner (1950). Originally described as occurring on fallen leaves, *C. aculeata* has been considered to typically occur on dead leaves of *Cladium mariscus* (Corner 1950, Hansen & Knudsen 1997). Specimens collected on bark or dead wood share a similar basidioma configuration, hyphae and spores.

As Corner (1950) suggested *Pistillaria mucedinea* is very close to *C. aculeata*. The small size of basidiomata (0.5–0.75 mm) and the 4-spored basidia described in the protologue support this view. Furthermore, our study of an authentic specimen kept at PC, collected on bark as described in the protologue, has scarcely septate thick-walled hyphae as observed in the material on *Cladium mariscus*. We agree with Corner (1950) and even suggest *P. mucedinea* might be conspecific with *C. aculeata* and list it as a possible earlier synonym. However, a better insight on species limits in *Ceratellopsis* needs to be acquired to further test this.

Names formerly placed in *Ceratellopsis* and imperfectly known, excluded here or illegitimate

Ceratellopsis aciculata (Durieu & Lév. ex Sacc.) Corner, Ann. Bot. Mem. 1: 200. 1950.

Basionym: *Pistillaria aciculata* Durieu & Lév. ex Sacc., Syll. Fung. 6: 759. 1887.

Typus: **Lectotype** designated here: Bory de Saint-Vincent & Durieu de Maisonneuve, Expl. Sci. Algérie 1(5): tab. 32, fig. 4. 1846. MycoBank MBT387461.

Notes: *Pistillaria aciculata*, published as a *nomen nudum* (Bory de Saint-Vincent & Durieu de Maisonneuve 1846), was invalid until Saccardo provided a description. The illustration provided by Bory de Saint-Vincent & Durieu de Maisonneuve (1846) shows brown, pointed acute structures that do not look like a fertile fungus but rather incipient basidiomata of a marasmiod fungus. This figure is, to our knowledge, the only original element and it is accordingly proposed as lectotype.

Ceratellopsis asphodeli (Pat.) Corner, Ann. Bot. Mem. 1: 203. 1950.

Basionym: *Ceratelya microscopica* var. *asphodeli* Pat., Cat. Pl. Cell. Tunisie: 66. 1897.

Typus: No type specimen in the Patouillard herbarium (FH, PC). No original illustration.

Notes: The 2-spored basidia and the presence of cystidia described in Patouillard (1897) suggest that *C. asphodeli* is a synonym of *Pterulicium gracile*. The pink tones can be present in *P. gracile* (Olariaga 2009).

Ceratellopsis biformis Khurana in Berthier, Bull. Soc. Linn. Lyon. 45: 190. 1976 [*nom. illeg.*, Art. 39, 40].

Notes: The description provided by Berthier (1976) based on Corner's notes of a fungus on *Quercus* leaves from India suggests that *C. biformis* may belong to *Ceratellopsis* as conceived here due to its narrow, 1.5–2 µm broad, medulla hyphae. Nevertheless, *C. biformis* was never validly published since neither a Latin diagnosis nor a type specimen were provided for it.

Ceratellopsis brondaei (Quélet) Corner, Ann. Bot. Mem. 1: 203. 1950.

Basionym: *Clavaria brondaei* Quélet., Revue mycol. (Toulouse) 14(54): 65. 1892.

Typus: No type specimen in PC and TL.

Notes: Quélet (1892) described *C. brondaei* apparently based only on the Brondeau plate no. 165 ("Alb. 165"). The illustration provided in the protologue (plate 126, fig. 3), probably a reproduction of plate no. 165, shows a small white clavarioid fungus, said to grow in forest on soil among tiny mosses. The description, except the ecology, tallies with a species of *Ceratellopsis* as treated here, but in the absence of microscopic information and a type specimen, a reliable interpretation cannot be provided, as Corner (1950) stated.

Ceratellopsis caespitulosa (Sacc.) Corner, Ann. Bot. Mem. 1: 203. 1950.

Basionym: *Pistillaria caespitulosa* Sacc., Atti del Congr. bot. di Palermo. 1902.

Typus: [from Saccardo, Syll. Fung. 17: 202. 1905]: **France**, Côte d'Or, in cortice emortuo *Lonicera periclymeni* [*Lonicera periclymenum*], PAD.

Notes: The denticulate "basidia" and the 1-septate biguttulate spores suggest that *C. caespitulosa* is an asexual morph fungus,

probably conspecific with *Isaria friesii* (Leotiomyces, Ascomycota).

Ceratellopsis carestiae (Ces.) Corner, Ann. Bot. Mem. 1: 203. 1950.

Basionym: *Pistillaria carestiae* Ces. in Bres. & Sacc., Malpighia 11: 255. 1897.

Typus: **Italy**, Piemonte, Alagna Valsesia, *sur ramis secchi Syringa vulgaris*, 13 Oct. 1857, Ab. Carestia no 27 (S-F15983 !, ex Bresadola herbarium; **lectotype** designated here, MycoBank MBT387464).

Notes: The material constitutes an asexual fungal state growing on bark, very probably conspecific with *Isaria friesii*. The spore content, described as divided in two ("*plasma bipartito*") is due, in fact, to the 1-septate spores, as in *C. caespitulosus* (see above).

Ceratellopsis corneri Berthier, Bull. mens. Soc. linn. Lyon 43: 188. 1974.

Typus: **France**, Lyon, Soucieu-en-Jarrest, *sur l'écorce pourrissante d'un arbre abattu* (Gymnosperme?), Bussy, 11 Apr. 1970 (**holotype** G).

Notes: Due to the 4–6 µm broad medulla hyphae and the amyloid spores, *C. corneri* does not conform to *Ceratellopsis*. We consider it that *C. corneri* should be examined and compared to *Mucronella* instead.

Ceratellopsis dryopteridis (S. Imai) Corner, Ann. Bot. Mem. 1: 203. 1950.

Basionym: *Pistillaria dryopteridis* S. Imai, Sapporo Trans. Sapporo nat. Hist. Soc. 13(4): 386. 1934.

Typus: **Japan**, Ishikari province, Nov. probably at SAPA.

Notes: The filiform 1–5 mm long basidiomata and 9–12.5 µm long spores suggest that *C. dryopteridis* should not be excluded from *Ceratellopsis*. The spores of *C. dryopteridis* are asperulate and therefore a relationship with *Pterula* is suggested here, but the type specimen, if it exists, should be examined to confirm this.

Ceratellopsis equiseticola (Boud.) Corner, Ann. Bot. Mem. 1: 204. 1950.

Basionym: *Pistillaria equiseticola* Boud., Bull. Trimestr. Soc. Mycol. France 33(1): 13. 1917.

Typus: **France**, Saône-et-Loire, Clovey (?), *ad caules Equiseti limosi* [*Equisetum fluviatile*], May 1915, Boudier herbarium (PC !, as *P. equisetina*; **lectotype** designated here, MycoBank MBT387465).

Notes: As earlier suggested by Berthier (1976), we conclude that *C. equiseticola* is a synonym of *P. gracile* after examining type material.

Ceratellopsis graminicola (Bourdot & Galzin) Corner, Ann. Bot. Mem. 1: 204. 1950.

Basionym: *Pistillaria graminicola* Bourdot & Galzin, Hymenomyc. France: 139. 1928.

Typus: No type specimen in the Bourdot & Galzin herbarium (PC). No original illustration.

Notes: The 12–18 µm long, 2–4-spored basidia, small spores (6–7 × 4 µm) and narrow, 1.5–2.5 µm broad hyphae given in the original description would indicate that *C. graminicola* should be

retained in *Ceratellopsis*, rather than being conspecific with *P. gracile*. It might be conspecific with *C. aculeata* or *C. acuminata*, but details on its hyphal structure are necessary to provide a solid interpretation.

Ceratellopsis helenae (Pat.) Corner, Ann. Bot. Mem. 1: 204. 1950.

Basionym: *Pistillaria helenae* Pat., Tab. Anal. Fung. 1: 26. 1883.

Typus: No type specimen in the Patouillard herbarium (FH, PC). **Lectotype** designated here: Patouillard, Tab. Anal. Fung. 1: fig. no. 57. 1883. MycoBank MBT387466.

Notes: The forked or sparsely branched basidiomata, with a tendency to be caespitose, and the presence of a distinct stipe, suggest that *C. helenae* is a synonym of *Typhula crassipes*. Although basidiomata of *T. crassipes* are usually simple, we have observed branched basidiomata as those depicted in the lectotype figure. Also, 2-spored basidia and incarnate tones are sometimes present in *T. crassipes* (Olariaga 2009). Corner (1950) compared *C. helenae* to *P. gracile*, but the latter lacks a stipe.

Ceratellopsis kubickae Pilát, Česká Mykol. 12(4): 217. 1958.

Typus: **Czech Republic**, prope Třeboň, *ad folium putridum Salicis auritae* [*Salix aurita*], 15 May 1958, Kubíčka (PRM 655767).

Notes: Pilát (1958) described *C. kubickae* as monomitic and compared it with *P. gracile*. Berthier (1976) investigated the type material and proposed that *C. kubickae* is a synonym of *P. gracile*, and that Pilát (1958) overlooked skeletal hyphae. In our opinion, the 2-spored basidia and the absence of a stipe in *C. kubickae* support it is a synonym of *P. gracile*.

Ceratellopsis mucosa (Berk. & M.A. Curtis) Corner, Ann. Bot. Mem. 1: 205. 1950.

Basionym: *Typhula mucosa* Berk. & M.A. Curtis, Grevillea 2(14): 18. 1873.

Typus: **USA**, South Carolina, Society Hill, in herb. mort., 1852, Carolina inf. No. 3832 (**syntypes** FH 596847, K).

Notes: The original description is very meagre, and we are unable to propose a reliable interpretation without checking type material. Corner (1950) failed also to provide a specific interpretation and stated that *C. mucosa* "may be *Ceratellopsis*, *Pterula*, or a rudimentary *Pistillaria*".

Ceratellopsis rickii (Oudem.) Corner, Ann. Bot. Mem. 1: 205. 1950.

Basionym: *Mucronella rickii* Oudem., Ned. kruidk. Archf., 3 sér. 2(3): 667. 1902.

Synonym: *Cnazonaria rickii* (Oudem.) Donk, Meded. Bot. Mus. Herb. Rijks Univ. Utrecht 9: 99. 1933.

Typus: **The Netherlands**, Limburg, Valkenburg, *in caulibus herbarum praesertim Asparagi off.* [*Asparagus officinalis*], May 1901, J. Rick, herb. Oudemans (**holotype** L). **Isotype:** Bourdot & Galzin herbarium (PC !).

Notes: Jülich (1980) reduced *C. rickii* to a synonym of *P. gracile* after examining type material. We confirm this synonymy based on characters seen on the cited isotype.

Ceratellopsis rosella (Fr.) Corner, Ann. Bot. Mem. 1: 206. 1950.

Basionym: *Pistillaria rosella* Fr., *Epicr. syst. mycol.*: 587. 1838. [1836–1838].

Typus: No type specimen in the Fries herbarium (UPS). No original illustration.

Notes: The pink colour described in the protologue is almost unique to *T. micans* among typhuloid fungi and we thus agree with Berthier (1976) in considering *C. rosella* a synonym of *T. micans*.

Ceratellopsis sydowii (Bres.) Corner, *Ann. Bot. Mem.* 1: 206. 1950.

Basionym: *Clavaria sydowii* Bres. in Sydow, *Hedwigia* 35: (61). 1896.

Typus: **Germany**, Saxony, Muskau, O.L. Bergpark, *ad ramulos Robiniae pseudoacaciae*, Jul. 1895, P. Sydow, *Mycoth.* March. 4405 (**syntypes** CHRb, MIN, NCU).

Notes: The caespitose growth habit on dicot. bark, pale pink colour (“dilute carnei”), long basidia (24–26 µm) and spore size mentioned in the protologue (9–10 × 5–5.5 µm) suggest that *C. sydowii* is a synonym of *T. crassipes*.

Ceratellopsis terrigena Berthier, *Bull. Soc. Linn. Lyon* 43(6): 188. 1974.

Typus: **France**, Rhône, Lyon, Izeron, sur terre nue d'un talus en sous-bois, 7 Aug. 1966, CL. 29 (**holotype** G).

Notes: Due to its 1.5–3.5 µm broad medulla hyphae *C. terrigena* does not conform to *Ceratellopsis* as here defined. Also, the presence of striking protruding cystidia is unknown for any other species of *Ceratellopsis*. The shape of cystidia and the absence of clamp connections may suggest *C. terrigena* to be allied with *Alloclavaria* in the *Rickenella* clade (*Hymenochaetales*).

Ceratellopsis thujicola (Kauffman) Corner, *Ann. Bot. Mem.* 1: 206. 1950.

Basionym: *Pistillaria thujicola* Kauffman, *Pap. Mich. Acad. Sci.* 9: 207. 1929 [1928].

Typus: **USA**, Michigan, Alger: Rock River, on inner side of *Thuja occidentalis* on loose bark, 8 Sep. 1927, C.H. Kauffman (**holotype** MICH11745).

Notes: The up to 10 mm long branched basidiomata do not conform clearly to *Ceratellopsis* as here defined, and we thus exclude it from this genus. The type material should be examined to propose a more precise interpretation.

Ceratellopsis tremula (Sacc.) Corner, *Ann. Bot. Mem.* 1: 207. 1950.

Basionym: *Pistillaria ferryi* subsp. *tremula* Sacc. in Sacc. & D. Sacc., *Syll. Fung.* 17: 202. 1905.

Typus: **Italy**, Padova, orto botanico Patavino, *ad fructum putrem Trichosanthis anguineae* [*Trichosanthes sanguinea*], ubi *Botrytis vulgaris* et *Acremoniella atra*, Feb. 1904 (**syntype** PAD).

Notes: The 3–5 mm long basidiomata, 2-spored basidia and 8–11 µm long spores conform to *P. gracile*, but the type specimen needs to be examined to confirm the synonymy. Although this synonymy is listed in *Index Fungorum* (2019, viewed on 11 June 2019), it has not been otherwise proposed to our knowledge.

Pleurotineae Aime, Dentinger & Gaya, *Biol. J. Linn. Soc.*: 10.1111/bij.12553, 16. 2015.

Phyllotopsidaceae Locquin ex Olariaga, Huhtinen, Læssøe, J.H. Petersen & K. Hansen, **fam. nov.** MycoBank MB831374.

Basidiomata pleurotoid or clavarioid and sometimes arising from a sclerotium. *Spore deposit* white to salmon pink. *Hyphal system* monomitic. *Basidiospores* hyaline, cylindrical, allantoid or subglobose, smooth, without iodine reactions. *Cheilocystidia* sometimes present in pleurotoid genera. *Clamp connections* present, rarely absent. Saprotrophic.

Type genus: *Phyllotopsis* E.-J. Gilbert & Donk ex Singer

Representative genera: *Macrotyphula*, *Phyllotopsis* and *Pleurocybella*.

Notes: *Macrotyphula*, *Phyllotopsis* and *Pleurocybella* were suggested to be closely related by Dentinger & McLaughlin (2006) and our analyses confirm that they form a monophyletic group. Despite this, no obvious synapomorphic characters support the relationship between the typhuloid *Macrotyphula* and the pleurotoid *Phyllotopsis* and *Pleurocybella* (Moncalvo *et al.* 2002). All three genera contain saprotrophic species, mostly lignicolous, and possess clamp connections.

Macrotyphula R.H. Petersen, *Mycologia* 64: 140. 1972. *nom. cons. prop.*

Type: *Clavaria fistulosa* Holmsk.: Fr. (synonym: *Macrotyphula fistulosa* (Holmsk.: Fr.) R.H. Petersen).

Synonyms: *Sclerotium* Tode, *Fung. mecklenb. sel.* 1: 2. 1790 : Fr., *Syst. Mycol.* 2: 246. 1822. *nom. rej. prop.* **Type:** *Sclerotium complanatum* Tode : Fr. (synonym: *Typhula phacorrhiza* (Reichard : Fr.) Fr.).

Clavariadelphus subgen. *Typhulopsis* Corner, *Ann. Bot. Mem.* 1: 692. 1950 [*nom. inval.* Art. 40.3, two species were indicated as type].

Macrotyphula megasperma (Berthier) Olariaga, Huhtinen, Læssøe, J.H. Petersen & K. Hansen, **comb. nov.** MycoBank MB831762.

Basionym: *Typhula megasperma* Berthier, *Bull. Soc. Linn. Lyon* 45: 78. 1976.

Macrotyphula phacorrhiza (Reichard : Fr.) Olariaga, Huhtinen, Læssøe, J.H. Petersen & K. Hansen, **comb. nov.** MycoBank MB831761.

Basionym: *Clavaria phacorrhiza* Reichard, *Schriften Berlin. Ges. Naturf. Freunde* 1: 315. 1780. [“*Clauaria phacorrhiza*”] : Fr., *Syst. mycol.* 1: 495. 1821.

Synonyms: *Sclerotium complanatum* Tode, *Fung. Mecklenb. Sel.* 1: 5. 1790.

Typhula phacorrhiza (Reichard : Fr.) Fr., *Observ. Mycol.* 2: 298. 1818. [“*Typhla*”].

Phacorrhiza filiformis Grev., *Scott. Crypt. Fl.* 2: 93. 1824 [*nom. nov.* based on *Clavaria phacorrhiza* Reichard]

Typhula phacorrhiza var. *complanata* (Tode) Sacc., *Syll. Fung.* 6: 745. 1888. [* *complanata*].

Typus: **Lectotype** of *Clavaria phacorrhiza*: Sowerby, *Col. Fig. Eng. Fung.* 2: tab. 233. 1798, as “*phacorrhiza*”, designated by Olariaga & Salcedo (2013: 42). **Lectotype** of *Sclerotium complanatum* designated here: Tode, *Fung. Mecklenb.* 1: tab. 1, fig.

9. 1790. MycoBank MBT387906. **Germany**, Bayern, Oberbayern, Landkreis Miesbach, valley Kleinthal near Miesbach, in a garden under *Ribes nigrum* and *Ribes rubrum*, on wet litter of various plants, mostly of *Ribes*, 2 Mar. 1992, F. Brand, *Microf. Exs.* No. 49 (UPS, as *Sclerotium complanatum*; **epitype** of *Sclerotium complanatum* designated here; **Isoepitypes** in B, BPI, CANB, DAOM, FH, GZU, H, HAL, HMAS, LE, M, MA, NMW, PRM, TNS). MycoBank MBT389352.

Specimens examined: **Austria**, prope Tullnerbach, in silva "Wiener Wald, ad petiolos *Fraxini excelsioris* L., C. de Keissler, Krypt. Exs. 1840 (PC, as *Sclerotium complanatum*). **France**, Pyrénées atlantiques, Borce, Le Gave d'Aspe, on the ground, among *Rubus idaeus* and *Myrrhis odorata*, 12 Oct. 2014, J.C. Zamora & I. Olariaga, IO.14.200 (S); without locality, dans les bois, parmi les tas de feuilles pourries, Desmazières, *Pl. Crypt. N. France, Ed. 1536* (PC, as *Sclerotium complanatum*). **Spain**, Navarre, Basaburua, Orokieta, Loiandi, on the ground among needles under *Picea abies*, 27 Oct. 2017, I. Olariaga, J. Martín, J. Teres & J.M. Riezu, ARAN-Fungi 7446. **Sweden**, Skåne, Eriksdal, Vitabäckskällan Nature Reserve, on wet ground under *Alnus*, 3 Oct. 2014, N.-O. Nilsson & I. Olariaga, IO.14.167 (S); Uppland, Uppsala-Näs, Vreta, in a compost-heap, 18 Oct. 1975, L. Jonsell, *Fung. Exs. Suec.* 3249 (PC).

Typhula phacorrhiza* var. *heterogenea Berthier, Bull. Soc. Linn. Lyon 45: 197. 1976.

Typus: **USA**, Idaho, Priest River, *inter foliis Alni tenuifoliae* [*Alnus tenuifolia*], 19 Oct. 1920, Weir 16943 (CGE, **holotype**).

Notes: This taxon, due to its gelatinised sclerotia with normal epidermoid layer (Berthier 1976), may also belong to *Macrotyphula*. The type material appears to have lost its basidiomata (Berthier 1976) and we find it premature to place it in *Macrotyphula*.

Pterulaceae Corner, Beih. Nova Hedwigia 33: 194. 1970.

Type genus: *Pterula* Fr. : Fr.

Representative genera: *Allantula*, *Coronicium*, *Dimorphocystis*, *Merulicium*, *Pterula*, *Pterulicium*.

Pterula Fr. : Fr., Syst. Orb. Veg. 1: 90. 1825.

Basionym: *Anthina* [unranked] *Pterula* (Fr.) Fr., Syst. Mycol. 3: 285. 1832: Fr., idem.

Type: *Pterula plumosa* (Schwein. : Fr.) Fr., selected by Donk (1954: 472).

Pterulicium Corner, Ann. Bot. Mem. 1: 699. 1950. *Type*: *Pterulicium xylogenum* Corner

Synonyms: *Ceratellopsis* Konrad & Maubl., Icon. Select. Fung. 6: 502. 1937. *Type*: *Ceratellopsis queletii* (Pat.) Konrad & Maubl. (synonym *Pterulicium gracile* (Desm. & Berk.) Leal-Dutra, Dentinger, G.W. Griff.), *typ. rej. prop.*

Deflexula Corner, Ann. Bot. Mem. 1: 695. 1950. *Type*: *Deflexula fascicularis* (Bres. & Pat.) Corner

Notes: Since the type of *Ceratellopsis* nests in *Pterulicium* (Fig. 3), the correct name for *Pterulicium* is *Ceratellopsis* under the current nomenclatural rules. A proposal to preserve the current usage of *Ceratellopsis* and *Pterulicium* is, however, in preparation (see Discussion).

Pterulicium gracile (Desm. & Berk.) Leal-Dutra, Dentinger & G.W. Griff. in Leal-Dutra, Griffith, Neves, McLaughlin, McLaughlin, Clasen & Dentinger, IMA Fungus 11(2): 15. 2020. *Basionym*: *Typhula gracilis* Desm. & Berk. in Berk, Ann. Nat. Hist., Ser. 1, 1: 202. 1838. ["*Typhula? gracilis*"].

Synonyms: *Clavaria gracilis* (Desm. & Berk.) P. Karst., Bidrag Kännedom Finlands Natur Folk 37: 181. 1882. ["*Cl? gracilis*"; *nom. illeg.*, later homonym of *Clavaria gracilis* Bolton and *C. gracilis* Pers. : Fr., Art. 53].

Pistillaria gracilis (Desm. & Berk.) Pat., Tab. Anal. Fung. 6: 30. 1887.

Ceratella gracilis (Desm. & Berk.) Pat., J. Bot. (Morot) 3: 36. 1889.

Hirsutella gracilis (Desm. & Berk.) Pat., Essai tax. Hyménomyc.: 50. 1900.

Pterula gracilis (Desm. & Berk.) Corner, Ann. Bot. Mem. 1: 514. 1950.

Clavaria microscopica Malbr. & Sacc., Michelia 2(6): 42. 1880.

Clavaria aculina Quél., Compt. Rend. Assoc. Franç. Avancem. Sci. 9: 670. 1881. ["1880"]

Pistillaria aculina (Quél.) Pat., Tab. Anal. Fung. 6: 29. 1887.

Ceratella aculina (Quél.) Pat., Hymenomyc. Eur.: 137. 1887.

Cnazonaria aculina (Quél.) Donk., Meded. Ned. Mycol. Ver. 22: 97. 1933.

Pistillaria queletii Pat., Tab. Anal. Fung. 1: 22. 1882.

Ceratella queletii (Pat.) Pat., Hymenomyc. Eur.: 137. 1887. [valid combination following Arts. 41.3 and 38.14].

Ceratellopsis queletii (Pat.) Konrad & Maubl., Icon. Sel. Fung. 6: 502. 1937.

Typhula brunaudii Quél., Compt. Rend. Assoc. Franç. Avancem. Sci. 13: 283. 1885. [1884].

Clavaria brunaudii (Quél.) Sacc., Syll. fung. 6: 730. 1888.

Ceratella ferryi Quél. & Fautrey, Revue. Mycol. (Toulouse) 15(57): 15. 1893.

Pistillaria ferryi (Quél. & Fautrey) Sacc., Syll. Fung. 11: 141. 1895.

Ceratella microscopica var. *asphodeli* Pat., Cat. Pl. Cell. Tunisie: 66. 1897.

Ceratellopsis asphodeli (Pat.) Corner, Ann. Bot. Mem. 1: 203. 1950.

Pistillaria attenuata Syd. & P. Syd., Hedwigia 39: (1). 1900.

Pistillaria acicula Bourdot & Galzin, Hymenomyc. France: 139. 1928. ["1927"].

Pistillaria juncicola Bourdot & Galzin, Hymenomyc. France: 138. 1928. ["1927"].

Typus: **UK**, without locality, ex Desmazières herbarium (PC, not found, **lectotype** designated in Corner (1950: 515) by type indication). **Isolectotype**: UPS (!).

Additional materials examined: **France**, Charente-Maritime, Saintonge, mais [*Zea mays*], P. Brunaud, Quélet herbarium (PC !, **lectotype** of *Typhula brunaudii* designated here, MycoBank MBT387470); Côte-d'Or, Noidan, sur tiges séchées de *Coix lacryma-jobi*, Fautrey, Jun. 1892, Fautrey Sel. Gall. Exs. no 6203 (PC !, **lectotype** of *Ceratella ferryi* designated here, **isolectotypes**: BR, ILL, MIN, UPS, MycoBank MBT387491); Rhône, Saint Priest, les Bouys, vers le Souey, "sur joncs [*Juncus*] purrissants", H. Bourdot, 27 Sep. 1918, Bourdot 24978 (PC !, **lectotype** of *Pistillaria juncicola* designated here, MycoBank MBT387471); Seine-Maritime, environs de Rouen, sur jonc [*Juncus*], Apr. 1880, A. Le Breton, Quélet herbarium (PC !, **lectotype** of *Clavaria aculina* designated here, MycoBank MBT387469); Seine-Maritime, Rouen, sur les joncs [*Juncus*] morts et humides, forêt de Noumare (?), A. Malbranche, (PC !, **lectotype** of *Clavaria microscopica* designated here, MycoBank MBT387468). **Germany**, Brandenburg, Finkenkrug pr. Nauen, ad folia culmosque graminum, *Calamagrostidis epigeii* [*Calamagrostis epigejos*], *Agrostidis albae* [*Agrostis alba*] etc., Mycoth. Mar. no. 4803 (S F15411 !, **lectotype** of *Pistillaria attenuata* designated here, **isolectotypes**: FH00608505 (!), MICH, MycoBank MBT387678). **Lectotype** of *Pistillaria queletii* designated here: Patouillard, Tab. Anal. Fung. 1: fig. 45. 1883. MycoBank MBT389354. **Sweden**, Skåne, Kristianstads kommun, Balsberget Nature Reserve, on dead standing *Juncus effusus* stalks, at damp place, N.-O.

Nilsson & I. Olariaga, 2 Oct. 2014, IO.14.142 (S, **epitype** of *Pistillaria queletii* designated here, MycoBank MBT387907).

Notes: In order to contribute to nomenclatural stability, an epitype specimen that represents *P. gracile* is proposed above for *Pistillaria queletii* (see Discussion). No good and recent specimen of *P. gracile* from France was available to epitypify *C. queletii*. Nevertheless, European material of *P. gracile* is morphologically and genetically homogeneous — ITS and 28S sequences available from France, Germany and Canada (CBS 309.79, CBS 325.58, CBS 554.85) are identical or nearly so to the sequences obtained by us from Sweden — and therefore we epitypify *C. queletii* using a specimen of *P. gracile* collected in Sweden.

Sarcomyaceae Olariaga, Huhtinen, Læssøe, J.H. Petersen & K. Hansen, **fam. nov.** MycoBank MB831375.

Basidiomata pleurotoid, with gelatinous context in pileus. Gills slightly decurrent, crowded, forking. Stem lateral, floccose. Spore deposit white. *Basidiospores* cylindrical to allantoid, amyloid. *Basidia* claviform, (2–)4-spored, clamped. *Cheilo-* and *pleurocystidia* fusiform to clavate, more or less thick-walled. *Pileipellis* and part of trama gelatinised. *Clamp connections* present. Saprotrophic, lignicolous.

Type genus: *Sarcomyxa* P. Karst.

Only genus: *Sarcomyxa*.

Notes: The family contains a single genus with unique pleurotoid basidiomata, gelatinised pileipellis, fusiform to clavate cheilo- and pleurocystidia and amyloid spores (Knudsen & Vesterholt 2012). Due to its isolated position within the *Pleurotineae* (Figs 2, 3), a new family is coined to accommodate *Sarcomyxa*.

Typhulaceae Jülich, Biblioth. Mycol. 85: 393. 1982 [“1981”]

Type genus: *Typhula* (Pers. : Fr.) Fr.

Typhula (Pers.) Fr., Obs. Mycol. 2: 296. 1818: Fr., Syst. Mycol. 1: 494. 1821, *nom. cons. prop.*

Basionym: *Clavaria* [unranked] *Typhula* Pers. : Fr., Syn. Meth. Fung. 1: XVIII. 1801

Type: *Typhula incarnata* Lasch, *typ. cons. prop.*

Synonyms: *Pistillaria* Fr., Syst. Mycol. 1: 496. 1821: Fr., *idem*.

Type: *Pistillaria micans* (Pers. : Fr.) Fr., selected by Clem. & Shear, Gen. Fungi: 345. 1931 (synonym *Typhula micans* (Pers. : Fr.) Fr.).

Cnazonaria Corda in J. Sturm, Deutschl. Fl., Pilze 2: 55. 1829.

Type: *Clavaria setipes* Grev. (synonym *Typhula gyrans* (Batsch : Fr.) Fr.).

Scleromitra Corda in Sturm, Deutschl. Fl., 3 Abt., 2: 59. 1829.

Type: *Scleromitra coccinea* Corda (synonym *T. micans* (Pers. : Fr.) Fr.).

Phacorhiza Pers., Mycol. Eur. 1: 192. 1822 : Fr., Syst. Mycol. 3 (Index): 140. 1832. *Type:* *Phacorhiza sclerotoides* (Pers. : Fr.) Pers. (synonym *Typhula sclerotoides* (Pers. : Fr.) Fr.).

Pistillina Qué., Compt. Rend. Assoc. Franc. Avancem. Sci. 9: 671. 1881. [“1880”]. *Type:* *Pistillina hyalina* Qué. (synonym *Typhula subhyalina* Courtec.).

Sphaerula Pat., Tab. Anal. Fung. 1: 27. 1883. *Type:* *Sphaerula capitata* Pat. (synonym *Typhula capitata* (Pat.) Berthier)

Gliocoryne Maire, Bull. Soc. Bot. France 55: 121. 1909. *Type:* *Clavaria uncialis* Grev. (synonym *Typhula uncialis* (Grev.) Berthier)

Dacryopsella Höhn., Anz. Kaiserl. Akad. Wiss. Wien, Math.-Naturwiss. Kl., Abt. 1, 124: 50. 1915. *Type:* *Dacryopsis typhae* Höhn. (synonym *T. subhyalina* Courtec.).

Tygervalleyomyces Crous, Persoonia 39: 387. 2017. *Type:* *Tygervalleyomyces podocarpi* Crous.

New combinations in *Typhula*

Typhula podocarpi (Crous) Olariaga, Huhtinen, Læssøe, J.H. Petersen & K. Hansen **comb. nov.** MycoBank MB831376.

Basionym: *Tygervalleyomyces podocarpi* Crous, Persoonia 39: 387. 2017.

Notes: The asexual and only known morph of *T. podocarpi*, described from South Africa, conforms to that of *Typhula crassipes*, described from Germany (Berthier 1976). The ITS region of *T. podocarpi* differs in 23 positions from that of European specimens of *T. crassipes* and we thus consider *T. podocarpi* to be a separate species.

Rickenellaceae Vizzini, Micol. Veg. Medit. 25(2): 144. 2010.

Type genus: *Rickenella* Raithel.

Representative genera: *Alloclavaria*, *Atheloderma*, *Blasiphalia*, *Bryopistillaria*, *Cantharellopsis*, *Contumyces*, *Cotylidia*, *Ginnsia*, *Globulicium*, *Gyroxylus*, *Loreleia*, *Muscinupta*, *Odonticium*, *Peniophorella*, *Resinicium*, *Rickenella*, *Sidera*, *Skvortzovia* and *Tsugacorticium*. Excluded from *Rickenellaceae*: *Repetobasidium*.

Notes: Genera in the *Rickenella* clade have been assigned to the *Repetobasidiaceae* (Zhang et al. 2018), often left without family assignment (Kirk et al. 2008, Knudsen & Vesterholt 2012), or included in the family *Rickenellaceae* (Begerow et al. 2018). Our analyses suggest that *Repetobasidium* does not nest in the *Rickenella* clade, and *Repetobasidiaceae* cannot therefore be used to accommodate genera in the *Rickenella* clade. Consequently, we adopt *Rickenellaceae* as the correct placement for genera in this clade, excluding *Repetobasidium* so that *Rickenellaceae* is not superfluous as when erected by Vizzini (2010).

Bryopistillaria Olariaga, Huhtinen, Læssøe, J.H. Petersen & K. Hansen, **gen. nov.** MycoBank MB831377.

Etymology: From ancient Greek (“*bryon*”, moss), referring to its habitat on bryophytes, and from *Pistillaria*, referring to its similarity with several species placed in that genus.

Biotrophic on mosses, and maybe in addition saprobic on dead leaves and culms. *Basidiomata* gregarious or fasciculate (2–5 basidiomata), simple clavarioid, 0.6–1 mm high, initially lanceolate and with sterile apex, then cylindrical or claviform, with rounded fertile apex, white. Stipe short or absent, cylindrical, glabrous or pubescent. Hyphal system monomitic. *Basidiospores* without iodine reactions, smooth. *Basidia* claviform, 16–21 µm long. *Medulla hyphae* parallel-arranged, cylindrical, septate, thin-walled, 3–4 µm broad, without iodine reactions. *Clamp connections* absent.

Type: *Bryopistillaria sagittiformis* (Pat.) Olariaga, Huhtinen, Læssøe, J.H. Petersen & K. Hansen

Bryopistillaria sagittiformis (Pat.) Olariaga, Huhtinen, Læssøe, J.H. Petersen & K. Hansen, **comb. nov.** Fig. 7. MycoBank MB831378.

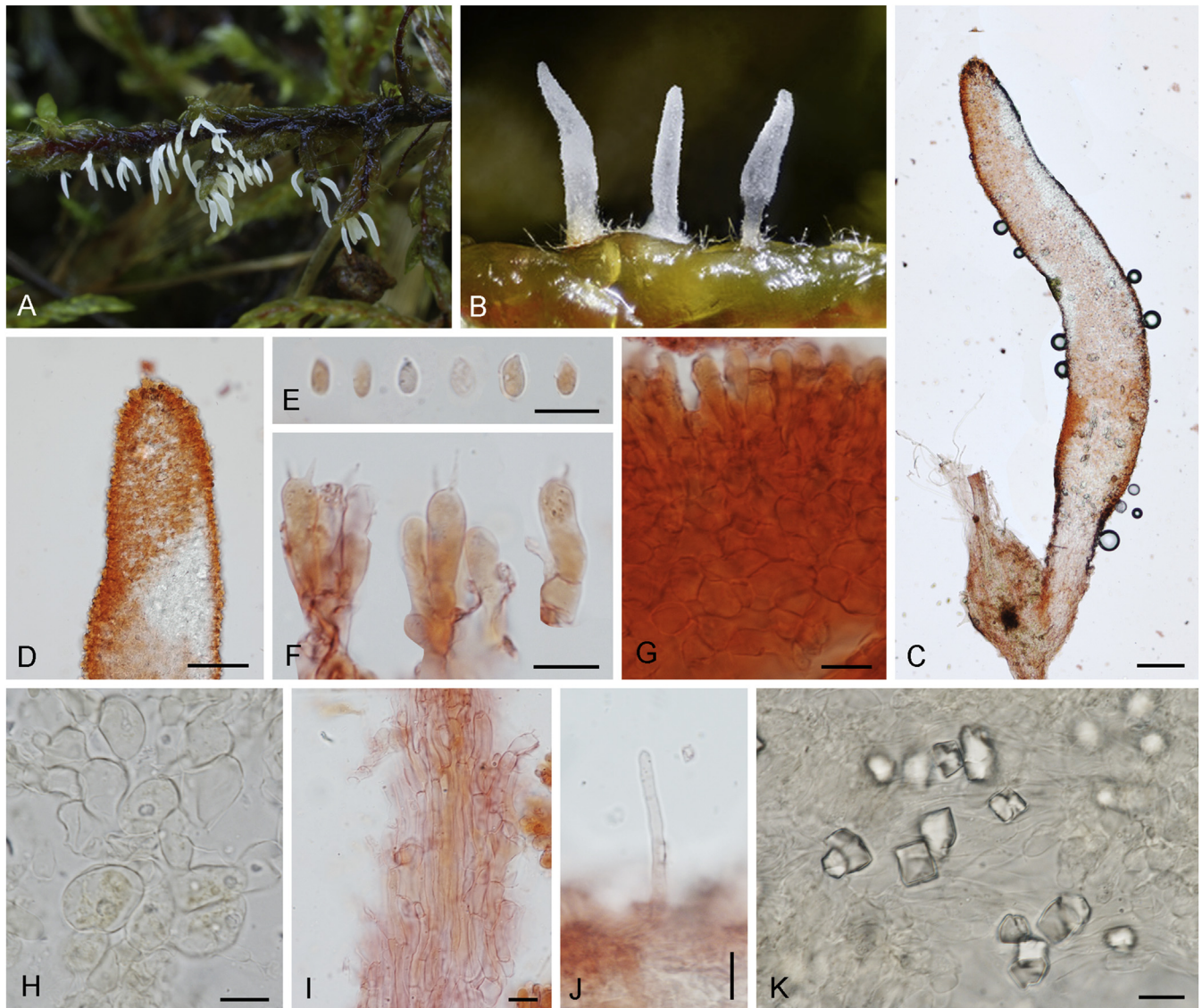


Fig. 7. *Bryopistillaria sagittiformis* (epitype, IO.15.85, S). **A.** Basidioma growth habit. **B.** Close-up of basidiomata. **C.** Basidioma observed using a light microscope. **D.** Close-up of basidioma apex. **E.** Basidiospores. **F.** Basidia. **G.** Hymenium section showing a subhymenium with globose to subglobose cells. **H.** Subhymenium cells. **I.** Thin-walled septate medullar hyphae. **J.** Caulinar hair. **K.** Crystals. Mounting media were Melzer's reagent (H, K) and Congo Red in ammonia (C–G, I–J). Scale bars: C = 100 µm; D = 50 µm; E–K = 10 µm. Photographs I. Olariaga, except B–C by J.H. Petersen.

Basionym: *Pistillaria sagittiformis* Pat., Tab. Anal. Fung. 1: 26. 1883 ["sagittæformis"]

Synonym: *Ceratellopsis sagittiformis* (Pat.) Corner, Ann. Bot. Mem. 1: 206. 1950. ["sagittæformis"].

Basidiomata gregarious or caespitose in groups of 2–5 basidiomata, 0.7–1.2 mm high, simple, with a short stipe. Fertile part narrowly claviform, sharply delimited from the stipe, white, 0.6–0.1 × 0.15–0.3 mm. Stipe short, cylindrical, glabrous or with sparse hairs, hyaline white, 0.1–0.4 × 0.1–0.2 mm. Subiculum spreading out on the substratum among basidiomata. Apex pointed and sterile in very young basidiomata, hyaline white, then obtuse and fertile. **Basidiospores** ellipsoid, sometimes in tetrads, hyaline, smooth, without iodine reactions, 4.5–6.5(–8) × 3–3.5(–4) µm. **Basidia** claviform, (1–2)-4-spored, 16–23 × 4.5–7 µm, clampless. **Subhymenium** composed of globose to subglobose hyphae, thin-walled, hyaline, 4–10(–12) µm broad. **Generative hyphae** cylindrical to fusiform, hyaline, thin-walled, clampless, 2.5–6(–9) µm broad, without iodine reactions. Hyphae on the stipe surface cylindrical, thin-walled, clampless, 3–3.5 µm broad. **Caulinar hairs** sparse,

cylindrical, thin-walled, up to 50 × 3 µm. Subiculum formed by cylindrical hyphae, thin-walled, straight, branching at right angles, clampless, 3–4 µm broad. Skeletal hyphae absent. **Crystals** sometimes present among the medulla hyphae, bipyramidal or sphaeroid. Attempts to obtain cultures from shed spores on MEA unsuccessful.

Typus: **Lectotype** designated here: Patouillard, Tab. Anal. Fung. 1: fig. 56. 1883. MycoBank MBT389355. **Estonia**, Otepää, Karula National Park, Peräjärve forest trail, on living *Pleurozium schreberi*, 13 Sep. 2015, I. Olariaga, IO.15.85 (S, **epitype** designated here; **isoeotype** in UPS). MycoBank MBT387918.

Known distribution: Denmark, Estonia, Finland, France, Sweden.

Additional materials examined: **Denmark**, Lolland, Biowide plot 120, Hejrede Sø, 5 Nov. 2014, T. Læssøe & T. Smidth, DMS-695059 (C); Sjælland, Allindelille Fredskov, on dead stem of *Alnus*, 20 Oct. 1977, H. Knudsen, C-F-124736; Amager Strandpark, on moss, 17 Nov. 2014, T. Læssøe, C-F-113951; Asserbo Plantage, on damp *Juniperus* bark and living mosses, 28 Feb. 2019, O. Martin, DMS-10005573 (C); Vestskoven, on damp *Juniperus* bark and mosses, 14 Feb. 2018, T. Kehlet, DMS-9242450 (C); Biowide plot 079, Melby Hede, 6 Nov. 2014, T. Læssøe, DMS-695405 (C); Biowide Plot 070, Gjessøvej, on moss, 31 Aug.

2015, T. Borgen & T. Læssøe, C-F-114679; Biowide plot 120, Hejrede Sø, base of *Poaceae* plant, 5 Nov. 2014, T. Læssøe & T. Smidth, C-F-114417; Strødam Reservatet, on mosses, rotten leaves and bark, 8 Nov. 2003, T. Læssøe, DMS-398331(C); Jægersborg Dyrehave, on moss and algae, 20 Jun. 1998, T. Læssøe, DMS-384562 (C-F-38168); Mons Klinteskov, v. Nælderenden, on moss on branch in damp hole, 23 Oct. 1971, H. Knudsen, C-F-94572; Stabjerggård, on *Tortula*, 14 Nov. 1976, H. Knudsen, C-F-94573. **Finland**, Pohjois-Häme, Laukaa, Hallalähde, on water dripping hillside west of the spring, on stock covered with moss, abundant on *Pleurozium schreberi*, 14 Sep. 2004, T. Rämä (TUR 178089). **France**, Pyrénées atlantiques, Escot, Le Barescou, on living mosses, 8 Oct. 2016, I. Olariaga (ARAN-Fungi 4625). **Sweden**, Dalarna, Särna, ca. 1.5 km W from Kryptjärnen, on living *Thuidium tamariscinum* and *Plagiomnium*, spreading on a dead herbaceous culm, 31 Aug. 2015, I. Olariaga, IO.15.41 (S); Skåne, Eriksdal, Vitabäckskällan Nature Reserve, on living leaves of *Scorpidium cossonii*, 3 Oct. 2014, N.-O. Nilsson & I. Olariaga, IO.14.164 (S); Skåne, Tomelilla, Årupkärets Nature Reserve, on living *Scorpidium cossonii*, in a fen, 3 Oct. 2014, N.-O. Nilsson & I. Olariaga, IO.14.163 (S); Uppland, Uppsala, the cemetery wall, southeast corner adjacent to Carolinaparken, on low mosses (*Tortula ruralis*), 12 Sep. 1932, S. Lundell (UPS F-152985, as *Ceratellopsis* cf. *sagittiformis*).

Notes: The original plate of *B. sagittiformis* shows a fungus with a fertile apex, 2-spored basidia and aseptate medulla hyphae reminiscent of skeletal hyphae. [Corner \(1950\)](#) suggested this plate might correspond to a *Pterula* species, but this view cannot be verified, as no type specimen appears to exist in the Patouillard herbarium (FH, PC). Instead, we interpret *B. sagittiformis*, as a species with obtuse fertile basidiomata at least when not extremely young, medulla hyphae 3–4 µm broad, lacking clamp connections and occurring usually, though apparently not strictly, on living mosses ([Hansen & Knudsen 1997](#)). It is possible that mosses are always present but not necessarily act directly as substrate for the basidiomata. Accordingly, we propose an epitype specimen to stabilise its current interpretation ([Corner 1950](#), [Hansen & Knudsen 1997](#)).

Key to genera that contain species that can be considered typhuloid

1. Lichenised; growing on a thallus containing green algae.....*Multiclavula*
1. Non-lichenised; not associated with green algae.....2
2. Basidia with transverse septa; on living bryophytes.....*Eocronartium muscicola*
2. Basidia without septa; on various substrates incl. bryophytes3
3. Clamp connections verticillate on context hyphae.....*Lutypha sclerotiophila*
3. Clamp connections absent or simple when present.....4
4. With a sclerotium.....5
4. Without a sclerotium.....7
5. With skeletal hyphae; smell phenolic when fresh.....unbranched forms of *Pterula sclerotiicola*
5. Without skeletal hyphae; smell not phenolic (living basidiomata).....6
6. Sclerotium compressed; sclerotial rind normal (i.e. with cells rooting in the medulla) with medulla gelatinised; basidiomata brown; fertile part cylindrical.....*Macrotyphula phacorrhiza* and *M. megasperma*
6. Sclerotium usually not compressed, sclerotial rind inverse (i.e. with cells not rooting in the medulla), if normal, with medulla rarely gelatinised; basidiomata brown or with other colours, fertile part cylindrical to convex.....*Typhula* p.p.
7. With skeletal hyphae.....8
7. Without skeletal hyphae.....9
8. Stipe absent; protruding hymenial cystidia producing conidia; basidia 2-spored; spores 9–16 × 3.5–7 µm; smell phenolic when fresh.....*Pterulicium gracile*
8. Stipe short; hymenial cystidia absent; basidia 1–4-spored; spores smaller; smell not phenolic.....*Ceratellopsis* p.p.
9. Spores ornamented.....*Ramariopsis* p.p.
9. Spores smooth.....10
10. With hymenial cystidia.....11
10. Without hymenial cystidia.....13
11. Fertile part more or less cylindrical; terricolous; clamps absent; caulocystidia absent.....“*Ceratellopsis*” *terrigena*
11. Fertile part globose to spatulate; on dead plant remnants; clamp connections sometimes present; caulocystidia sometimes present.....12
12. Spores ellipsoid, fusiform or sigmoid.....*Physalacria*
12. Spores broadly ellipsoid to subglobose.....*Actiniceps* (= *Chaetotyphula*)
13. Basidiomata < 2 mm high; apex sterile and pointed at least in young basidiomata.....14
13. Basidiomata higher, if < 2 mm high then apex fertile even in young basidiomata.....15
14. Medulla hyphae < 2.5 µm broad; subhymenial hyphae not swollen, < 2.5 µm broad; on dead plant remnants; clamps (always?) present.....*Ceratellopsis* p.p.
14. Medulla hyphae 2.5–6(–9) µm broad; subhymenial hyphae globose to subglobose, 4–10(–12) µm broad; often on living mosses; clamps absent.....*Bryopistillaria sagittiformis*
15. Basidiomata pale brown; usually > 10 mm high; spores inamyloid.....*Macrotyphula* p.p.
15. Basidiomata if > 10 mm high then colour not brown; spores amyloid or not.....16
16. Clamps present and abundant on hyphae in the context.....17

16. Clamps absent or restricted to basidia and loop-like.....19
17. Not positively geotropic; fertile part and stipe usually sharply delimited; growing usually on dead leaves or stems of plants.....*Typhula* p.p.
17. Usually positively geotropic; fertile part and stipe not clearly differentiated; growing on highly decayed wood or pores.....18
18. With gloeocystidia; spores subglobose.....*Dentipratulum*
18. Without gloeocystidia; spores ellipsoid.....*Mucronella*
19. Basidiomata < 1.5 mm high; stipe with 150–250 µm long erect hairs with obtuse ends; on dead wood.....*Hirticlavula elegans*
19. Basidiomata larger, hairs absent or considerably shorter; terrestrial or on leaves and herbaceous remnants of plants.....20
20. On plant remnants; spores usually amyloid.....*Typhula* p.p.
20. Terrestrial; spores non-amyloid.....*Clavaria*

DISCUSSION

Evolution of typhuloid fungi and family delimitation in the *Agaricales* and the *Pleurotineae*

This study provides the most robust phylogenetic hypothesis for typhuloid fungi to date, and it resolves for the first-time relationships with other genera in the *Agaricales*. Terminal nodes recovered in our *Agaricales* analyses using ML and Bayesian approaches are consistent to a great extent with those obtained by Matheny *et al.* (2006). In addition, several more basal nodes received support when analysed using a Bayesian method (Figs 2, 3), while ML bootstrap values were low for most of those. As RAXML does not allow for a free model-choice, the same dataset was analysed using IQ-TREE (Nguyen *et al.* 2015) and Garli (Zwickl 2006), but the supported topology was identical and bootstrap values were similar to those obtained in RAXML. It has long been known that Bayesian PP tend to be higher than ML bootstrap values (e.g. Susko 2009), and have been claimed to refer to different properties of phylogenetic confidence (García-Sandoval 2014). Although our dataset is the most comprehensive ever assembled for typhuloid fungi, it might still contain too little molecular characters to reconstruct the comparatively deep divergences among clades. In any case, it was highly expected that novel supported topologies would be recovered for the first time when more taxa were added to the analyses, even if many nodes so far only received support in the Bayesian analyses.

Typhulaceae, *Pleurotaceae*, *Pterulaceae*, *Stephanosporaceae*, *Sarcomyxa*, *Pleurocybella* and *Phyllotopsis* are resolved as a monophyletic group for the first time (Figs 2, 3), corresponding to the *Pleurotineae* (Dentinger *et al.* 2016). Our results confirm that *Sarcomyxa* and the *Typhulaceae* belong to *Pleurotineae* as anticipated by Dentinger *et al.* (2016). The back-bone of the *Pleurotineae* phylogeny is fully resolved (Fig. 3) and suggest that *Macrotyphula* and *Typhula*, with a typhuloid basidioma configuration, might have evolved from a pleurotoid ancestor. The phylogenetic relationships of *Phyllotopsis*, *Pleurocybella* and *Sarcomyxa*, of debated family placement, are also resolved in our Bayesian *Pleurotineae* phylogeny (Fig. 3). These three pleurotoid genera have been placed, not always together, in families containing white-spored agarics, such as *Marasmiaceae*, *Mycenaceae*, *Pleurotaceae* and *Tricholomataceae* (e.g. Jülich 1982, Moncalvo *et al.* 2000, Kirk *et al.* 2008, Begerow *et al.* 2018), or even *Pterulaceae* (Begerow *et al.* 2018), but previous phylogenies did not support any of these family placements

(e.g. Matheny *et al.* 2006, Binder *et al.* 2010). Based on our phylogenies and the high Bayesian PP (Figs 2, 3), we propose the new family *Sarcomyxa* to encompass *Sarcomyxa* and validate the family *Phyllotopsidaceae* to accommodate *Macrotyphula*, *Phyllotopsis* and *Pleurocybella*. On the other hand, *Pterulaceae* and *Radulomycetaceae*, recently split sister families (Leal-Dutra *et al.* 2020), contains an assemblage of fungi with clavarioid, corticioid and polyporoid basidioma types (Zhao *et al.* 2016), monomitic or dimitic, defined as “morpho-anatomically a very diverse family with colourless spores” (Begerow *et al.* 2018), but well-supported in molecular phylogenies (Fig. 3; Matheny *et al.* 2006, Binder *et al.* 2010). All members of *Pterulaceae* and *Radulomycetaceae* studied when fresh (*Aphanobasidium filicinum*, *Pterula subulata*, *Pterulicium gracile*, *P. scleroticola*, *Radulomyces confluens*, *R. molaris*, and *R. rickii*) had a distinct phenolic or naphthalene odour, as sometimes described for *P. multifida* (e.g. Petersen 1999). It is thus suggested here that such an odour, produced by a probably unidentified fungal metabolite, may be a synapomorphic character of *Pterulaceae*, but further species must be tested to draw a final conclusion.

According to our results, the hygrophoroid clade as recovered by Matheny *et al.* (2006), is not monophyletic, because the *Hygrophoraceae*, the *Pleurotineae* and *Xeromphalina campanella*, all previously assigned to the hygrophoroid clade (Matheny *et al.* 2006), are encompassed in three independent lineages within the *Agaricales* (Fig. 2). The position of the *Hygrophoraceae* inferred from our analyses is not consistent with the 208-locus phylogeny by Dentinger *et al.* (2016), which placed *Hygrocybe conica* (*Hygrophoraceae*) and *Clavaria fumosa* (*Clavariaceae*) in a monophyletic group described as the *Hygrophorineae*. The dataset employed by Dentinger *et al.* (2016) contained 36 taxa of the highly diverse *Agaricales* and only a single taxon of the *Hygrophoraceae*. Phylogenetic analyses of a matrix with few taxa, even when the number of overall characters is large, can be subject to strong systematic biases and can be susceptible to long-branch attraction (Heath *et al.* 2008). In our preliminary analyses, *H. coccinea* nested in *Clavariaceae* when no other *Hygrophoraceae* were included in the matrix. With the addition of a few taxa of the *Hygrophoraceae* (Fig. 2), *Clavariaceae* and *Hygrophoraceae* do not form a monophyletic group, but are suggested to be successive sister taxa to the rest of the *Agaricales*. Our data indicates that Dentinger *et al.* (2016) recovered *H. conica* and *C. fumosa* in a monophyletic clade due to a long-branch attraction artifact and we anticipate that this clade will no longer be resolved when more species of *Hygrophoraceae* are included in phylogenomic

analyses of large multigene datasets. Following our phylogenetic hypothesis, we propose the new suborder *Clavariineae* to accommodate the *Clavariaceae*.

Typhula phacorrhiza* is a synonym of *Sclerotium complanatum* that nests in *Macrotyphula

Earlier hypotheses on the phylogenetic position of *Typhula* and *Typhulaceae* relied on a misidentified specimen of *T. phacorrhiza* (DSH96-059; Pine *et al.* 1999) that belongs to the *Macrotyphula juncea* species complex (Olariaga *et al.* in prep.). Therefore, this is the first time that *T. phacorrhiza* is included in a multigene phylogenetic study. As previously suggested, based on morphology (Olariaga & Salcedo 2013), *T. phacorrhiza* and *Sclerotium complanatum* belong to *Macrotyphula*. The bulk of species of *Typhula* form a distinct separate clade (referred to as the *Typhula*-core clade). Thus, our analyses confirm that the selection of *T. phacorrhiza* as type of *Typhula* is unfortunate (Berthier 1976, Olariaga & Salcedo 2013), also for the sake of nomenclatural stability. The examination of material deposited in herbaria under *S. complanatum* showed that this name is usually applied to sclerotia of *T. phacorrhiza* (e.g. Pl. Crypt. N. France, ed. 1, no 536; Microf. Exs. no 49; Krypt. Exs. no 1840; see material examined under *T. phacorrhiza*) and that *S. complanatum* is a synonym of *T. phacorrhiza* as proposed long ago (Remsberg 1940). Furthermore, the *Typhula*-core clade contains the types of all genera segregated from *Typhula* at some point. Based on analyses of a more inclusive species sampling of *Typhula* (Olariaga *et al.*, in prep), we consider it more appropriate to merge all those genera, as done by some authors (Berthier 1976, Knudsen & Vesterholt 2012), rather than splitting *Typhula* into several genera that could be recognised only with great difficulty.

A strict application of nomenclatural rules in the light of our phylogenetic hypothesis (Figs 2, 3) would result in a high number of undesirable name changes. The correct generic name for species of *Macrotyphula* and *T. phacorrhiza* would be *Sclerotium*. However, the adoption of *Sclerotium* for *Macrotyphula* species would be misleading, because nearly all *Macrotyphula* species lack sclerotia and *Macrotyphula* is a well-established name. At the same time, species in the *Typhula*-core clade would need to be transferred to *Pistillaria*, the oldest alternative genus name for the group. Pathogenic species of *Typhula*, such as *T. idahoensis*, *T. incarnata* or *T. ishikariensis*, on which extensive literature has been published, would undergo name changes. Also, the epithet of *T. incarnata* would need to be changed to avoid creating a later illegitimate homonym of *Pistillaria incarnata* Desm. In order to preserve nomenclatural stability, two proposals are in preparation to conserve: 1) *Typhula* with *T. incarnata* as conserved type, and 2) *Macrotyphula* against *Sclerotium* (Olariaga *et al.* unpubl.). In accordance with our proposals, we combine in *Macrotyphula* two closely related taxa treated by Berthier in *Typhula* subgen. *Typhula*: *T. phacorrhiza* and *T. megasperma*.

***Ceratellopsis s. auct.* is polyphyletic and misapplied**

Despite our efforts to find good material, very few specimens of *Ceratellopsis* were available for this study. Besides those types examined by Berthier (1976), only a few more type specimens of *Ceratellopsis* could be located and examined. The type specimens of most names placed in *Ceratellopsis* appear to be lost and

can only be interpreted through their protologues. Most non-type specimens of *Ceratellopsis* were characterised by having a central medulla of narrow, thick-walled hyphae, a poorly differentiated subhymenium of cylindrical < 2 µm broad hyphae, a sterile basidioma apex, a well-delimited stipe, basidia < 20 µm long and spores < 8 µm long. Some of these collections had skeletal hyphae in the medulla, as also observed in the type specimens of *C. acuminata*, while other specimens assigned to *C. aculeata* and *C. mucedinea* had scarcely septate hyphae with thinner walls. Specimens identified as *C. sagittiformis* differed in having broader (up 3–4(–8) µm), more often septate medulla hyphae, a well differentiated subhymenium with swollen, globose to subglobose hyphae (4–10(–12) µm) and a basidioma apex becoming fertile. Three type specimens (*C. attenuata*, *C. equiseticola* and *C. rickii*) and several other specimens filed under the names *C. aculeata* and *C. acuminata* represent *P. gracile*, because they possessed skeletal hyphae, 2-spored basidia, acuminate cystidia and lacked a stipe. As earlier suggested (Corner 1950, Berthier 1976), several names originally described or combined in *Ceratellopsis* represent in fact *P. gracile*.

This study provides the first molecular data of *Ceratellopsis*. It resolves the genus as polyphyletic, with species belonging to both the *Clavariaceae* and the *Hymenochaetales*. Among the specimens sampled for the molecular phylogenetic study, those with a sterile pointed apex and narrow thick-walled medulla hyphae nest in the *Clavariaceae*. This position is supported by the fact that tiny clavarioid basidiomata are also known in other *Clavariaceae*, such as in *Hirticlavula* (Petersen *et al.* 2014) and *Mucronella* (Birkebak *et al.* 2013). Narrow hyphae on the base of the stipe, typical in *Clavariaceae* (Olariaga 2009), have also been observed in species of *Ceratellopsis*. For the first time, we demonstrate that skeletal hyphae are present in some species of *Ceratellopsis* and that it is not a unique character for *Pterulaceae* among typhuloid fungi. The species of *Ceratellopsis* placed in *Clavariaceae* differ from *P. gracile* in having basidia < 20 µm long, a well-delimited stipe and in lacking protruding acuminate cystidia. This lineage of *Ceratellopsis* conforms to Corner's (1950) concept of *Ceratellopsis*, i.e. "*Ceratellopsis aculeata* and the species which appear to resemble it", except for the presence of skeletal hyphae in some species. The examination of a specimen identified as *C. aculeata* by Corner (PC), with very narrow, scarcely septate medulla hyphae, confirms this view. In accordance with this, we conclude that *C. corneri* and *C. terrigena*, having medullar hyphae 4–6 µm and 1.5–3.5 µm broad, respectively, do not belong to this lineage and must be placed elsewhere (see Taxonomy).

The inclusion of *C. sagittiformis* in the *Rickenella* clade of the hymenochaetoid clade is a novel and unexpected find although material identified as *C. sagittiformis* is often associated with living bryophytes, as several members of the clade are (Korotkin *et al.* 2018). The *Rickenella* clade encompasses fungi with a diverse basidioma configuration (agaricoid, clavarioid, cyphelloid, telephoroid, corticioid, etc.) that often are associated with mosses (Larsson *et al.* 2006). Within the *Rickenella* clade, *C. sagittiformis* resembles *Muscinaupta laevis* in having white basidiomata, in growing on living bryophytes and in lacking clamp connections (Eriksson & Ryvarden 1975, as *Cyphellostereum laeve*), but our phylogenetic analyses lack support to confirm a close relationship. Phylogenetic relationships within the *Rickenella* clade were previously explored using only ribosomal nuclear markers (5.8S and 28S; Larsson *et al.* 2006), and only recently using also the *RPB2* region. Even with the addition of

the 18S and the *RPB2* regions and more taxa to the analyses of the hymenochaetoid clade, relationships within the *Rickenella* clade remain largely unresolved (Korotkin *et al.* 2018, Fig. 5). The three specimens of *C. sagittiformis* have identical sequences and formed a distinct lineage. Based on this and the fact that *C. sagittiformis* is the only bryophilous, reduced clavarioid species known to belong to the *Rickenella* clade, we propose the new genus *Bryopistillaria* to accommodate it (see Taxonomy).

Proposing a reliable and stable interpretation of *C. queletii*, type of *Ceratellopsis*, is necessary to be able to provide a solid interpretation of *Ceratellopsis*. The name *Ceratellopsis queletii* appears not to have been employed since its original description (Patouillard 1883). Regrettably, no type specimen exists in PC and FH (G. E. Tocci pers. comm.) and no original specimen is likely to be present in any other fungarium. The absence of a stipe, the sterile apex, the 2-spored basidia and the presence of protruding acuminate cystidia, clearly depicted in the original illustration of *C. queletii* selected here as lectotype, are characteristic of *P. gracile* (Corner 1950, Berthier 1976, Jülich 1980). The spore size estimated by Corner from the original Patouillard plate of *C. queletii* is smaller ($6 \times 3 \mu\text{m}$) than the range we have estimated ($8\text{--}8.5 \times 4.5\text{--}5 \mu\text{m}$) and the size reported by Quélet ("8 μm ?", 1884) for *C. queletii*. Spores in *P. gracile* are generally reported as slightly larger than our measure estimates from the Patouillard plate, but those are almost within the ranges published for *P. gracile*: $9\text{--}16 \times 4\text{--}7 \mu\text{m}$ (Corner 1950), $10.5\text{--}12.5 \times 5.5\text{--}5.6 \mu\text{m}$ (Berthier 1976), $10\text{--}14 \times 5.5\text{--}6.5 \mu\text{m}$ (Jülich 1980) and $8\text{--}11 \times 5\text{--}7 \mu\text{m}$ (Daniëls & Moreno-Arroyo 2007). Based on all this, we consider *C. queletii* a synonym of *P. gracile*, as already Corner (1950) suggested.

Leal-Dutra *et al.* (2020), using one of the specimens of *P. gracile* employed in our analyses (CBS 309.79), showed that it belongs to the *Pterulicium* clade. This taxonomic conclusion reduces *Pterulicium*, as recently circumscribed, to a later synonym of *Ceratellopsis* and the forty-six names combined in *Pterulicium* (Leal-Dutra *et al.* 2020), besides its type *Pterulicium xylogenum*, would have to be combined again in *Ceratellopsis*. In addition, a new genus name would be required for *C. acuminata* and *C. aculeata*. In order to avoid nomenclatural changes that may cause confusion, a proposal to conserve *Ceratellopsis* with *C. acuminata* as conserved type is in preparation. The acceptance of this proposal would preserve the current usage of *Ceratellopsis* and *Pterulicium*, typified by *P. xylogenum*, a presumed causal agent of culm rot disease of bamboo (Harsh *et al.* 2005) and possibly also of sugarcane (Corner 1952).

CONCLUSIONS

This study reveals that typhuloid fungi appeared several times among the *Agaricomycetes* and contributes to the understanding of fungal evolution and shifts of basidioma configuration. Novel phylogenetic hypotheses are provided for several groups of typhuloid fungi and pleurotoid agarics, and pertinent family and generic classifications are proposed. Future phylogenomic analyses will hopefully incorporate more taxa, including typhuloid fungi, and will serve to further test our phylogenetic hypotheses.

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